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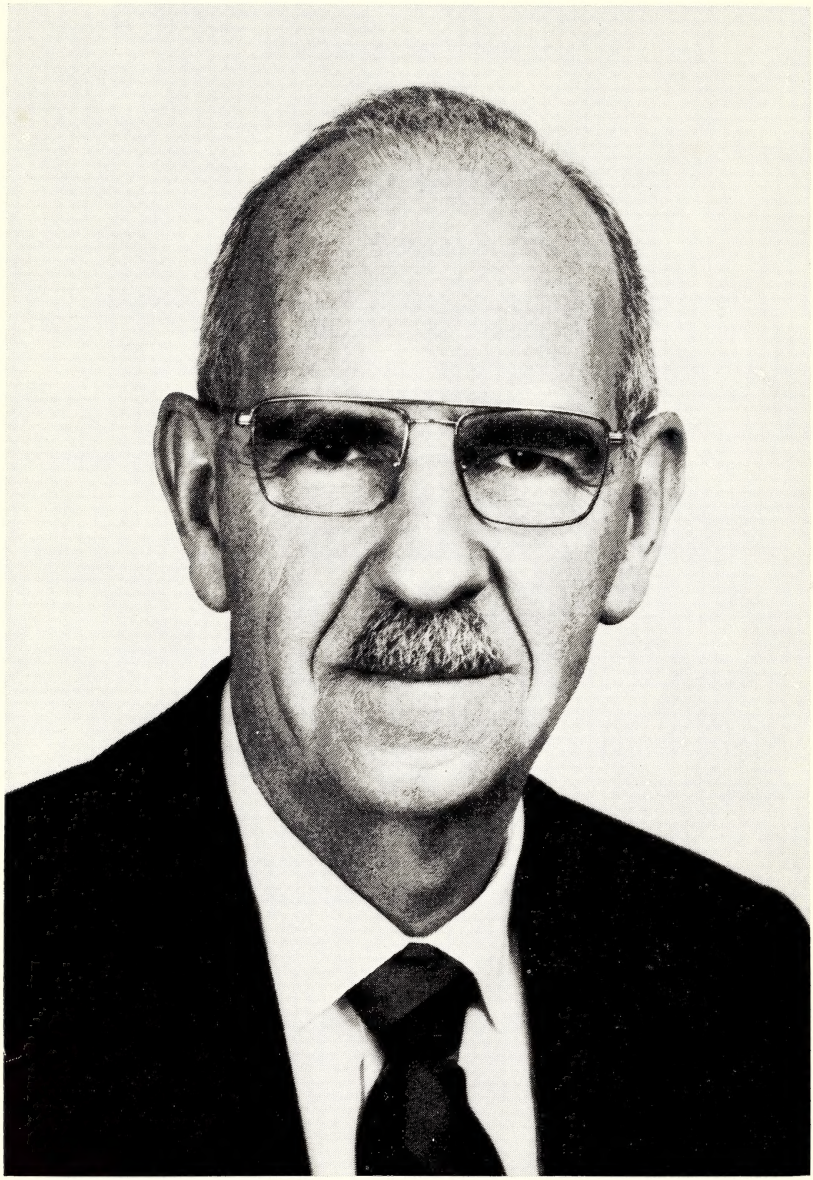

Volume 23 of Madroño is dedicated to Lincoln Constance, Professor of Botany, University of California, Berkeley, in recognition of his contributions to our knowledge of western American plants, particularly his taxonomic studies on Umbelliferae and Hydrophyllaceae, and for the leadership he has exerted in the botanical community.

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ERRATUM

p. 3. Formula for Community Quality Index should read:

$$\text{CQI} = \sqrt{\%\text{ total perennial cover} \times \%\text{ of total perennial cover by long-lived species}}$$

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EFFECTS OF PIPELINE CONSTRUCTION ON CREOSOTE BUSH SCRUB VEGETATION OF THE MOJAVE DESERT

F. C. Vasek, H. B. Johnson, and D. H. Eslinger
Department of Biology, University of California, Riverside 92502

Pipeline construction involves trenching, piling, and refilling operations and clearly constitutes a major disturbance of soil and plant cover. The effect on plant cover is one of nearly complete destruction. Revegetation does occur and its rate probably correlates inversely with the degree of aridity in a disturbed area. However, quantitative estimates of revegetation and recovery rates following pipeline construction have not been made for the Mojave Desert. Accordingly vegetation along a pipeline was surveyed and analyzed to obtain a data base from which to assess the impact of pipeline construction, estimate the indicated recovery rate, and suggest the course of secondary succession in creosote bush scrub vegetation.

We selected the Southern California Gas Company natural gas pipeline of 1960 for study because it provides a twelve year recovery reference frame. (Mr. Vlasek of the Southern California Gas Company in Victorville, California, kindly supplied background information on the pipeline). The pipe was laid in a trench 183 cm deep and 152.5 cm wide and then covered over with screened backfill and leveled. The right-of-way includes an access road, the trench line, and the berm.

The pipeline segment selected for study travels a utility corridor from Newberry to Lucerne Valley, San Bernardino County, California. We sampled the vegetation in ten areas along a 33.8 km segment of the pipeline right-of-way. The native vegetation in most of the study area consists of creosote bush scrub, which is the characteristic plant community on most of the Mojave Desert except for salt flats and higher mountains. (Plant community and species nomenclature follows Munz, 1959 and 1968.)

In each sample area four belt transects were made, each 50 m by 2 m. Two transects served as controls and two transects served to estimate the effects of disturbance. The four transects in each area were located as follows: A) about 50 m east and parallel to the trench line in undisturbed vegetation, as assessed visually; B) approximately 50 m west of the trench line in representative vegetation and not necessarily parallel to the trench; C) on the berm, that is, along the pipeline right-of-way where trench soil had been piled and then scraped away to refill the trench; and D) directly over the pipeline where trenching had produced the most severe disturbance. (The fourth transect is nearly 48 cm wider than the trench.)

Madroño, Vol. 23, No. 1, pp. 1–64. January 2, 1975.

The four transects in each sample area were each read by measuring and recording the distance across each perennial plant. Assuming that, on the average, plants cover a circular ground area, the ground cover area was calculated from the radius for each plant and summed for each species. On the few transects where small perennial herbs were extremely abundant their number was counted in two to four representative 0.5 m^2 plots and extrapolated to the area of occurrence within transects to estimate density and ground cover. The first four areas were sampled in July, 1972, following a relatively dry winter and prior to the full influence of 1972 summer rains. The last six areas were read in November, 1972, following a summer of fairly heavy precipitation and following several early winter storms. The ten sample areas (Table 1) are located sequentially southwest from Newberry at distances of 0.0, 4.8, 10.1, 14.6, 19.8, 20.6, 22.9, 26.2, 30.1, and 34.4 km. Direct comparisons among the ten

TABLE 1. PHYSICAL CHARACTERISTICS OF SAMPLE AREAS. [a] Marked change in slope between control transects 1 and 2; [b] Evidence of excessively heavy grazing by livestock; [c] Evidence of moderate soil salinity; [d] Marked vegetation discontinuities in vicinity.

Sample area	Topographic location	Exposure and slope	Surface stability	Substrate origin	Substrate composition	Surface heterogeneity	Elevation (m)
1	Broad wash	N.E. Gentle	Active erosion	Alluvium	Rocky	Moderate	600
2	Hillside	E. Moderate	Old erosion	Bedrock	Large to small rocks	High	670
3	Hillside[a]	N. Level to moderate	Stable	Residual	Small rocks	Low	950
4	Narrow wash[a]	.....	Active wash	Alluvium	.....	High	1050
5	Valley bottom[b c]	Level	Stable	Alluvium	Fine sand	Low	1160
6	Valley bottom[b d]	S.E. gentle	Stable	Alluvium	Sandy	Low	1190
7	Upper fan[b]	N.E. gentle	Stable	Alluvium	Rocky sandy	Low	1250
8	Hillside	S.W. gentle	Light erosion	Residual	Rocky	Moderate	1310
9	Lower fan	N.E. gentle	Slight erosion	Alluvium	Sandy	Low	1310
10	Middle fan	N.W. moderate	Slight erosion	Alluvium	Gravelly sand	Low	1100

sample areas are generally inappropriate because of variation in substrate, slope, and aspect (Table 1). Accordingly, primary comparisons are restricted to the four transects within each area. Comparisons among the ten samples are secondary.

The four transects were first compared by Jaccard's coefficient of community similarity (Phillipps, 1959) and then by an index we propose to call a Community Quality Index (CQI). We assume that the ecological quality of an area (Suffling et al., 1974) is a product of the community age and the site productivity. Our rationale is based on the premise that consistent, long-term productivity is maximized by stable populations and favorable environmental conditions and that older plant communities are less quickly replaced than younger ones (Suffling et al., 1974). Accordingly, an estimate of productivity, namely ground cover area, and an estimate of relative community age, namely the proportion of ground cover area provided by long-lived species, are integrated by way of their product. As a convenient scaling factor, the square root is extracted to yield:

$$\text{CQI} = \sqrt{\begin{array}{c}\%\ \text{Ground covered by}\\ \text{long-lived perennials}\end{array} \times \begin{array}{c}\%\ \text{Total perennial}\\ \text{ground cover}\end{array}}$$

The CQI takes into account the successional status of a community and can be applied objectively in assessing ecological quality and potential environmental impacts. Application of the CQI requires assignment of observed species to successional or to functional categories. In the case of creosote bush scrub communities, we recognize four functional groups of perennial plants and assign species to these groups on the basis of our own observations and judgment. The four groups are long-lived perennials, short-lived pioneer shrubs, pioneer perennial herbs, and other perennials. The species observed in our study, together with the number of plants recorded on our study plots, are each assigned to one of the functional groups in Table 2.

Long-lived perennials are known or judged on the basis of size or long-term observations (e.g., Shreve and Hinckley, 1937) to live over many decades or perhaps even centuries. In addition, plants of these species generally respond negatively to disturbance. Pioneer shrubs generally are soft shrubs or subshrubs that are known or judged to have relatively short life spans, probably not exceeding one or two decades. In addition, pioneer shrubs respond positively to disturbance by invasion and rapid increase in population size. Pioneer perennial herbs are also active invaders of disturbed sites and develop very large populations. In our area, the occurrence of large populations is irregular perhaps relating to the irregularity of summer rainfall, after which germination typically occurs, or to some other environmental factor. Lastly we recognize a group of "other perennials" consisting of perennial herbs and suffrutescent plants whose functional or successional status is not clear. We suspect many are pioneers that grow with winter rains.

TABLE 2. PERENNIAL SPECIES GROUPED IN FOUR FUNCTIONAL CATEGORIES AND LISTED IN ORDER OF ABUNDANCE.

	Number of individuals recorded		Number of individuals recorded
LONG-LIVED PERENNIALS		PIONEER SHRUBS	
Ambrosia dumosa (Gray) Payne	113	Hymenoclea salsola T. & G.	5,222
Larrea tridentata (Sesse & Moc. ex DC.) Cov.	107	Gutierrezia microcephala (DC.) Gray	9
Hilaria rigida (Thurb.) Benth. ex Scribn.	95	Haplopappus cooperi (Gray) Hall	5
Thamnosma montana Torr. & Frem.	73	Bebbia juncea Greene	4
Ephedra californica Wats.	62	Eriogonum fasciculatum Benth.	2
Opuntia ramosissima Engelm.	22	Viguiera deltoidea Gray	1
Lycium andersonii Gray	22	PIONEER PERENNIAL HERBS	
Yucca schidigera Roezl ex Ortgies	20	Euphorbia polycarpa Benth.	5,132
Echinocereus engelmannii (Parry) Ruempl.	7	Tridens pulchellus (HBK) Hitchc.	1,075
Dalea spinosa Gray	6	OTHER PERENNIALS	
Salazaria mexicana Torr.	4	Sphaeralcea ambigua Gray	103
Krameria parvifolia Benth.	4	Eriogonum inflatum Torr. & Frem.	24
Echinocactus polycephalus Engelm. & Bigel.	3	Dyssodia cooperi Gray	16
Opuntia echinocarpa Engelm. & Bigel.	3	Muhlenbergia porteri Scribn.	13
Yucca brevifolia Engelm. in Wats.	3	Mirabilis bigelovii Gray	3
Atriplex canescens (Pursh) Nutt.	2	Allionia incarnata L.	3
Cassia armata Wats.	2	Stephanomeria pauciflora (Torr.) Nutt.	2
Acacia greggii Gray	1	Sarcostemma hirtellum (Gray) R. Holm.	1
		Nicotiana trigonophylla Dunal in A. DC.	1

RESULTS

Most of the long-lived plants observed in this study belong to the following species: *Ambrosia dumosa, Larrea tridentata,* and *Hilaria rigida*. In addition, *Thamnosma montana* and *Ephedra californica* were commonly observed, but the remaining species of long-lived perennials were uncommon (Table 2). The second category includes short-lived pioneer shrubs that occur sporadically in the creosote bush scrub community usually in washes or other naturally disturbed areas. They also occur as major colonizers in more drastically disturbed areas. *Hymenoclea salsola* is the most abundant of these species but other pioneer shrub species contribute slightly to the total number of plants observed (Table 2). The third functional category includes pioneer perennial herbs such as *Euphorbia polycarpa* and *Tridens pulchellus*. Both species germinate in great abundance after summer rains. *Euphorbia* populates sandy, disturbed areas and *Tridens* populates flat, pebbly or rocky areas, particularly where run-off might accumulate. The fourth functional category

of perennial plants includes suffrutescent and herbaceous perennials. Most of those observed in our study belonged to *Sphaeralcea ambigua* and *Eriogonum inflatum*. In addition, small numbers of *Dyssodia cooperi* and *Muhlenbergia porteri* were observed; the remaining species (Table 2) are very sparse. *Sphaeralcea* and *Dyssodia* tend to occur on both the disturbed and undisturbed areas so their successional status is unclear. The remaining plants in this category are too few to form a pattern from which a more definitive judgment can be made.

The undisturbed vegetation alongside the pipeline right-of-way as well as the regenerating vegetation on the disturbed pipeline right-of-way was recorded in terms of the number and size of its constituent plants. An analysis of those data in terms of total perennial ground cover and the percent of the total cover made up by long-lived perennials, pioneer shrubs, and other perennials is shown in Table 3. In addition, the percentage of total perennial ground cover contributed by *Larrea* and *Ambrosia* is also shown in Table 3 for each of the transects. Plant density generally correlates with ground cover and is not analyzed further.

Considerable variation occurs among the ten sample areas. Although the general vegetation in most of the study area can be called creosote bush scrub, the percentage of the perennial ground cover on the control transects varies from 0 to nearly 94 percent for *Larrea* and from 0 to nearly 27 percent for *Ambrosia*. Total ground cover on the control transects ranges from 2.21 to 19.98 m^2 per transect of 100 m^2. Such variations probably reflect local differences in topography, slope, exposure, elevation, substrate, and probably general climate (see Table 1). The area traversed by the pipeline crosses the Newberry and portions of the Ord Mountains. Most of the northern locations are in very rough terrain, and the six northern ones are located in rain shadows of local mountains. The southern four sample areas are located southwest of East Ord Mountain on much gentler terrain and at fairly high elevations suggesting better growing conditions or higher site quality. A few more particular characteristics (Table 1) indicate that the vegetation of the ten sample areas cannot be directly compared but rather comparisons should be made among the four transects at each area. First, the two control transects from each area are compared by means of Jaccard's coefficient of similarity (Table 4). Generally, a similarity coefficient of approximately 0.7 or higher is considered an indication of virtual identity. The two control transects in the ten study areas have similarity coefficients ranging from 0.34 to 0.82. In sample areas 1, 4, 7, 8, 9, and 10, the similarity coefficients for the two control transects are above 0.64 and we will accept that value as indication of identity. Differences in the physical characteristics within study areas 2, 3, 5, and 6 can account for the dissimilarity between the control transects (Table 1). In sample area 2 the topographic heterogeneity is sufficient to explain that fairly low similarity coefficient. At sample area 3, transect B in the flat to the north of the pipeline should have a higher ground cover than does transect A on the

TABLE 3. ANALYSIS OF PERENNIAL GROUND COVER BY TRANSECT IN TEN SAMPLE AREAS.

Sample area	Total perennial cover, m^2	% Long-lived plants	% Pioneer shrubs	% Pioneer herbs	% Other perennials	% Larrea	% Ambrosia
			Transect A (Control)				
1	4.21	57.96	30.16	0.00	11.88	48.69	9.26
2	6.78	90.70	0.74	0.15	8.41	50.88	5.60
3	2.48	100.00	0.00	0.00	0.00	64.52	15.32
4	7.65	96.21	3.66	0.00	0.13	41.05	0.00
5	3.64	64.84	22.25	0.00	12.91	0.00	17.58
6	2.92	25.34	63.01	0.34	11.30	0.00	9.93
7	14.62	35.91	58.62	0.00	5.47	1.64	0.89
8	14.65	90.78	8.46	0.75	0.00	21.64	0.00
9	16.67	98.80	0.78	0.00	0.42	63.41	21.78
10	19.86	100.00	0.00	0.00	0.00	93.71	3.37
			Transect B (Control)				
1	5.99	75.79	24.21	0.00	0.00	42.40	8.34
2	3.04	99.34	0.00	0.00	0.66	51.64	25.99
3	6.88	85.76	14.24	0.00	0.00	85.76	0.00
4	4.50	95.56	0.00	0.00	4.44	36.22	0.00
5	2.21	10.86	84.62	0.00	4.52	0.00	9.05
6	2.72	86.03	6.25	0.00	7.72	0.00	5.51
7	19.98	65.36	29.93	0.00	4.70	8.01	0.30
8	11.69	85.03	9.32	4.28	1.37	0.00	1.54
9	10.02	97.41	0.00	0.30	2.29	49.40	26.95
10	14.46	100.00	0.00	0.00	0.00	93.02	6.98
			Transect C (Berm)				
1	6.32	18.35	81.49	0.16	0.00	0.47	0.00
2	1.63	4.29	95.71	0.00	0.00	0.00	4.29
3	1.15	0.00	98.26	0.00	1.74	0.00	0.00
4	8.09	0.00	87.14	0.00	12.86	0.00	0.00
5	0.89	0.00	83.15	12.36	4.49	0.00	0.00
6	0.17	0.00	17.65	0.00	82.35	0.00	0.00
7	12.25	0.00	99.18	0.16	0.65	0.00	0.00
8	4.52	3.98	48.01	46.90	1.11	0.22	0.00
9	2.05	98.54	0.00	0.00	1.46	50.24	48.29
10	9.41	8.08	0.11	91.82	0.00	0.00	8.08
			Transect D (Trench)				
1	5.13	0.39	99.42	0.19	0.00	0.00	0.39
2	0.08	0.00	100.00	0.00	0.00	.0.00	0.00
3	0.00	0.00	0.00	0.00	0.00	0.00	0.00
4	3.25	15.38	56.00	0.00	28.62	0.00	0.00
5	0.32	0.00	87.50	6.25	6.25	0.00	0.00
6	0.00	0.00	0.00	0.00	0.00	0.00	0.00
7	9.31	21.05	75.94	0.11	2.90	21.05	0.00
8	3.95	21.01	70.13	6.58	2.28	20.00	0.00
9	0.62	59.68	0.00	0.00	40.32	0.00	59.68
10	11.25	30.22	0.00	69.78	0.00	29.60	0.62

TABLE 4. JACCARD'S COEFFICIENT OF SIMILARITY FOR PAIRS OF TRANSECTS IN EACH OF TEN SAMPLE AREAS. Based on summation of coincident ground cover for each species.

Sample area	Transects compared					
	A/B	A/C	A/D	B/C	B/D	C/D
1	0.727	0.247	0.276	0.403	0.261	0.893
2	0.536	0.029	0.015	0.030	0.000	0.094
3	0.342	0.000	0.000	0.244	0.000	0.000
4	0.709	0.037	0.145	0.032	0.181	0.462
5	0.393	0.344	0.152	0.503	0.237	0.529
6	0.348	0.110	0.000	0.118	0.000	0.000
7	0.680	0.644	0.558	0.376	0.536	0.660
8	0.642	0.160	0.234	0.223	0.145	0.512
9	0.658	0.216	0.050	0.335	0.070	0.300
10	0.823	0.046	0.219	0.064	0.264	0.767
Mean	0.5868	0.1833	0.1649	0.2328	0.1694	0.4217
Standard deviation	0.1698	0.1963	0.1717	0.1687	0.1677	0.3158

slope to the south. The low coefficient for sample area 5 can probably be explained on the basis of disturbance by cattle grazing and for sample area 6 on the basis of a break in vegetation associated with the approach to the dry lake (Table 1). Despite some differences between two control transects, we believe that combining them provides a reasonable estimate of potential productivity of the vegetation on the pipeline because of the intermediate location.

Generally low coefficients of similarity occur between either of the control transects and either of the disturbed transects (Table 4) except in sample area 7. Comparisons between the two disturbance transects, that is transect C on the berm and transect D on the trenchline, are highly heterogeneous ranging from 0 to 0.89, suggesting that the vegetation on the two disturbed transects is sometimes very similar and sometimes very different. The similarities between transects C and D may be due to high percentages of pioneer shrubs or high percentages of pioneer herbs as in study area 10 (Table 3), and the differences may be due to greater cover on one or the other. Relative to each other the two disturbance transects show no consistent pattern for any parameter.

The Community Quality Index (CQI) has been calculated for each transect (Table 5) and provides another means of comparing vegetations on the several transects at each sample area. The CQI ranges from 8.60 to 44.56 for control transect A, and from 4.90 to 38.03 for control transect B. In both cases sample areas 5 and 6 have the lowest quality index and they occur in and near a dry lake where substantial disturbance of soil and vegetation by cattle is evident. The three northern sample areas have fairly low quality indices, probably because of gener-

TABLE 5. COMMUNITY QUALITY INDEX FOR EACH OF FOUR TRANSECTS (A, B, C, AND D) AND THE COMBINED CONTROL AND COMBINED DISTURBED TRANSECTS FOR EACH OF TEN SAMPLE AREAS (1 THROUGH 10). Ratios indicate the percentage similarity between the designated indices. * = reciprocal of column heading.

	Community Quality Index						CQI Ratios		
Sample area	A	B	C	D	A + B	C + D	B/A	D/C	$\frac{C+D}{A+B}$
1	15.62	21.30	10.77	1.41	18.68	7.68	0.73*	0.13	0.41
2	24.80	17.38	2.64	0.00	21.41	1.82	0.70	0.00	0.09
3	15.75	24.29	0.00	0.00	20.47	0.00	0.65*	0.00	0.00
4	27.13	20.70	0.00	7.07	24.16	5.00	0.76	0.00*	0.21
5	15.36	4.90	0.00	0.00	11.41	0.00	0.32	0.00	0.00
6	8.60	15.30	0.00	0.00	12.41	0.00	0.56*	0.00	0.00
7	22.91	36.14	0.00	14.00	30.26	9.90	0.63*	0.00*	0.33
8	36.47	31.53	4.24	9.11	34.09	7.11	0.86	0.47*	0.21
9	40.58	31.29	14.21	6.08	36.24	10.95	0.77	0.43	0.30
10	44.56	38.03	8.72	18.44	41.42	14.42	0.85	0.47*	0.35
Mean	25.18	24.09	4.06	5.61	25.06	5.69	0.68	0.15	0.19
Standard deviation	12.02	10.31	5.31	6.61	10.13	5.17	0.16	0.22	0.16

ally low ground cover, which in turn probably reflects the relatively low elevation and location in local rain shadows. The three southernmost sample areas have the highest quality indices, which probably reflects the higher ground cover associated with fairly high elevations and fairly good physical location and good rainfall. Sample areas 4 and 7 remain as intermediates. The general quality indices can be summarized by combining the data for transects A and B in each sample area and then calculating the CQI in Table 5.

The CQI for transect C over the berm ranges from 0, on half of the sample areas, to 14. Clearly these indices are substantially below the corresponding CQI for the control transects. The CQI for transect D over the trench ranges from 0 to 18, which is much lower than the vegetation on the control transects and is surprisingly slightly higher than the CQI's for vegetation on the berm. Since both transects C and D were on areas that have been subjected to severe disturbance at the same time, their combination is justified for comparison with the potential vegetation at that site. On this basis, the combined transects C and D have CQI's that range from 0 to 14 (Table 5), and the combined CQI for transects A and B ranges from 11 to 41 (Table 5).

Each CQI can be compared with any other CQI by striking a ratio between them. Control transects A and B have a quality ratio ranging from 0.32 to 0.86. Similarly, the ratio between CQI's for transects C and D range from 0 to 0.47. In both cases, the direction of difference between transects A and B and between transects C and D varies more or less at random as indicated by the expression of four ratios as recip-

rocals (Table 5); in other words, sometimes transect A has a higher CQI than transect B and transect C sometimes has a higher CQI than transect D, and vice versa. However, the combined transects C and D as a ratio of the combined transects A and B always fall between 0 and 1, which means that disturbed transects always have a lower CQI than control transects. The combined quality ratio for the two disturbed transects against the two undisturbed transects is probably the best one single estimate of impact, revegetation, and quality of vegetational recovery.

For sample area 1 the CQI ratio of disturbed transects to undisturbed transects is rather high (0.41). Since this is in an actively washing alluvial fan, a significant component of disturbance is part of the natural situation. Accordingly, the impact of pipeline construction at that site is not as drastic as it is elsewhere. At sample area 2 the disturbed vegetation is only nine percent of the quality of the undisturbed vegetation, probably because this area has a very stable substrate and a very high percentage of long-lived perennials. Sample area 3 has zero percent similarity of the disturbed site to the undisturbed site. Both are relatively poor, but there is no recovery, no invasion, and no revegetation of the disturbed sites by long-lived perennials. Similar interpretation pertains to areas 5 and 6. Sample areas 7 to 10 have higher percentages of similarities between the disturbed sites as compared with the undisturbed sites, probably due to the higher general productivity of those sample areas.

Discussion

Two aspects of this study may be considered in further detail. One is the assessment of vegetational recovery from the impact of pipeline construction. The second concerns aspects of plant succession as elucidated by this study. We know that this pipeline was constructed twelve years prior to our observations. We can assume that the two undisturbed transects represent the vegetation as it occurred prior to disturbance, and we also know that pipeline construction results in virtually the complete destruction of vegetation along that construction right-of-way.

Starting with a baseline of no vegetation we note that the long-lived perennials, after 12 years, comprise 0 to 41 percent of the ground cover on the pipeline right-of-way as the same species do in adjacent undisturbed vegetation. Therefore, significant revegetation has occurred by long-lived species at sample areas 1, 7, 9, and 10 for which quality ratios of 0.41, 0.33, 0.30, and 0.35 have been calculated and at sample areas 4 and 8 for which quality ratios of 0.21 have been calculated. On the other hand, quality ratios of 0.00 were calculated for sample areas 3, 5, and 6 and a quality ratio of 0.09 was calculated for sample area 2. The latter four areas clearly have not exhibited significant progress toward revegetation.

Characteristics associated with higher revegetation rates vary somewhat from one area to another. Sample area 1 had only a moderate pro-

ductivity to begin with and therefore did not have an advanced successional revegetation target.

Areas 9 and 10 have high productivity and therefore good growing conditions, probably in terms of soil quality, rainfall amount, and rainfall regularity. Area 7 has high productivity but a low percentage of long-lived perennials.

In contrast, areas 2, 3, 5, and 6 have low productivity. The poor growing conditions are doubtless associated with very low precipitation and at areas 2 and 3 probably with poor, rocky soil. The low initial quality associated with the low percentage of long-lived perennials at areas 5 and 6 does not compensate for the very low productivity as very little revegetation of any kind occurred there. Revegetation, therefore, occurs best in areas of high productivity or at least moderate productivity plus vegetational heterogeneity (i.e., intermediate community age).

The time required for vegetation to regain its original condition in terms of composition and ground cover is difficult to assess. Clearly, the vegetation in sample areas with low quality ratios will not regain predisturbance conditions in the foreseeable future. Vegetation in sample areas with quality ratios of 0.30 to 0.40 might be expected to regain predisturbance conditions in something like 2.5–3.5 times the elapsed time from disturbance to observation, or about 30–40 years if successional vegetative growth approximated a straight line relationship. However, since growth curves are not straight lines and soil conditions on the pipeline are sometimes drastically different from predisturbance soil conditions, 30–40 years is far too optimistic an estimate of regeneration time. Since growth curves typically are sigmoid in shape, slow initial regeneration, rapid intermediate development during an exponential phase, and then slow and very slow development during senescence or during an asymptotic approach to final conditions would be expected, especially in sites with very high percentages of long-lived species. On this interpretation the quality ratios of 0.30 to 0.40 probably represent a point in some portion of the exponential growth phase. Duration of that phase is unknown, but eventually the population will enter a prolonged senescent or asymptotic phase. Consequently, some other regeneration time estimate is necessary.

Another estimate of time required for complete regeneration could be provided by the average age of the plants destroyed. For this purpose, the age of creosote bushes would be most pertinent but only a few creosote bush age estimates are known to us. The best documented estimates (Chew and Chew, 1965) are for plants in an expanding population in southern Arizona where historical observations indicate recent invasion. The oldest plants in this population approach an age of 90 years. For large shrubs near Tucson, Arizona, Shreve and Hinckley (1937) estimate ages "well in excess of 100 years" on the basis that little change in size or bulk occurred during the course of a 30-year photographic record. Finally, Barbour (1969) notes the essential absence of age distribution

data and then simply uses plant height to determine age structure within populations. Barbour (1969) also describes the possibility that *Larrea* bushes may be aggregated because of asexual reproduction. He indicates that seedlings or young shrubs do not grow as close together as members of large clumps and therefore the clumps do not develop from (groups of) seedlings in close association.

Our observations agree with those of Barbour and extend the description of vegetative reproduction to the formation of "clonal rings" at least in the Mojave Desert. The common pattern of growth involves the death of older branches as a consequence of drought (Runyon, 1934), and their replacement by new branches that arise from the periphery of the old root crown. Accordingly, the center of a creosote bush dies and is replaced by new stems that eventually form new crowns peripheral to the original central crown. Over long periods of time with repeated cycles in which old stems die and new stems and new crowns are formed peripherally, the creosote bush growth pattern results in a ring of satellite clumps around a circular to elliptic sterile center. We have observed in our study area a continuous series of stages from single-stemmed young creosote bushes, to large clumps with dead branches in the center, to rings of satellite clumps. Among the latter, the size of the sterile center ranges up to several meters.

The radial spread growth pattern and the size distribution of clonal creosote rings in a population remains the subject of an active investigation and further elaboration is premature. However, the time required for the formation of large creosote rings must be enormous and our preliminary estimates suggest time periods in the range of 1500 to 3000 years for a creosote ring with a sterile center 1 m in radius. These estimates are based on the observation that successive crowns of small Mojave Desert creosote bushes are about 3 cm apart. If a crown reaches a span well in excess of 100 years as suggested by Shreve and Hinckley (1937) then a creosote ring with a sterile center 1 m in radius will have grown through about 30 increments in about 3000 years. Some verification of general longevity of creosote bushes is provided by a wood fragment taken from the center of a creosote ring with a sterile center 30 cm in diameter. This wood fragment was carbon dated (University of California, Riverside, Radiocarbon Lab Sample 154) at 585 $\pm$ 150 years or about 39 years per cm of radius. That plant is growing on a south-facing rocky hill in the Sacramento Mountains of San Bernardino County, California, a site of fairly low productivity more or less comparable to our study area 2 or 3. Doubtless, creosote bushes would grow faster on more favorable sites. These age considerations, however, suggest that old stable *Larrea* populations may include clonal creosote rings of considerable antiquity. In those cases, vegetational recovery from drastic disturbance would not be expected for several millennia, if at all.

The second consideration concerns the course of secondary plant succession. Following severe disturbance of the type under study, plants like

Hymenoclea salsola and species of *Euphorbia* invade and become established on the disturbed soil. Clearly they represent an early stage in succession. Of particular interest, however, is the fact that these species already constitute a significant fraction of the extant vegetation. Thus, *Hymenoclea,* with other pioneer shrubs, constitutes 0 to 85 percent of the vegetation, in terms of ground cover, on the undisturbed (by pipeline construction) transects and the pioneer perennial herbs also occur in small numbers on the undisturbed transects. The pioneers, then, seem to be short-lived species that normally occur in slightly disturbed situations, like small washes, in the creosote bush scrub community. A similar successional pattern was described by Wells (1961) for the abandoned streets of a desert ghost town. In this context, then, it may be significant to remember that the pioneer species ordinarily are slightly more abundant and cover greater ground on the berm than over the trench line (Table 2). Thus, the less severe disturbance of the berm may be more nearly similar to the natural disturbance of a desert wash. These species, therefore, thrive when the long-lived plants of the creosote bush scrub are removed. However, deep soil disturbance, e.g. a trench, is again less favorable for their growth. On the other hand, we note that plants like *Larrea tridentata* and especially *Ambrosia dumosa* are not completely eliminated from disturbed areas. We conclude, then, that the species of the mature creosote bush scrub community have some capability as pioneers, and that the primary pioneer species form a small but significant fraction of the mature creosote bush scrub community. Thus, a characteristic of the creosote bush scrub community is that its species are probably adapted in varying degree to continual, but relatively slight disturbance. Within this relatively sparse vegetation there is always some open ground subject to soil shifting, wind and water erosion, and other similar slight disturbances, and stands of creosote scrub occur in a variety of successional stages. Short-lived perennials, such as *Hymenoclea* and *Euphorbia* always have suitable sites in which to persist, at least in low numbers.

Desert vegetation then, as exemplified by the creosote bush scrub community, is fragile and easily destroyed, but does have a long term potential, probably measured in many centuries, for recovery from even drastic disturbance such as a pipeline.

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A NEW SPECIES OF GALIUM (RUBIACEAE) FROM COAHUILA

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The following new *Galium* was discovered in connection with work toward a flora of the Chihuahuan Desert, currently in preparation at the University of Texas.

Galium carmenicola Dempster, sp. nov. Herba perennis polygama semiprostrata. Caules foliaque hispida, sed inflorescentiae glabrae. Folia quaterna, ad 6 mm longa, anguste lanceolato-oblanceolata pungentia adscendentia, costa subter prominente. Flores plurse in ramulis brevibus subterminalibus, pedicellis brevissimis. Corollae campanulatae, glabrae, ultra dimidio fissae, segmentis apicibus tenuibus. Fructus sicci pilis crassiusculis aliquantum curvatis obtecti.

Type: Coahuila, Mina El Popo, ca 2 km S of Cañon El Diablo on dissected east slope of Sierra del Carmen, on steep slopes of massively-bedded limestone, 1600 m, 29 Jul 1973, *Johnston, Chiang, Wendt, and Riskind 11921.* Holotype: UC! (1400211); isotypes: MEXU, TEX.

Galium carmenicola is a slender, trailing, moderately congested, somewhat pungent plant. Flowers and fruits are very small, the corollas clearly and broadly campanulate, of a pale color (perhaps pink), the lobes reflexed. Fruits on the type specimen are few, most of the flowers apparently having been staminate, with small sterile ovaries and obsolete styles and stigmas. Pistillate flowers were not seen, and their styles and stigmas are therefore unknown. The fruits have stoutish hairs about one-fourth to one-third as long as the diameter of the fruit. Since the distinction between *Galium* species with uncinate fruit hairs and those with straight fruit hairs or none is generally a sharp and reliable means of separating species groups, *G. carmenicola* is disturbing, with most fruit

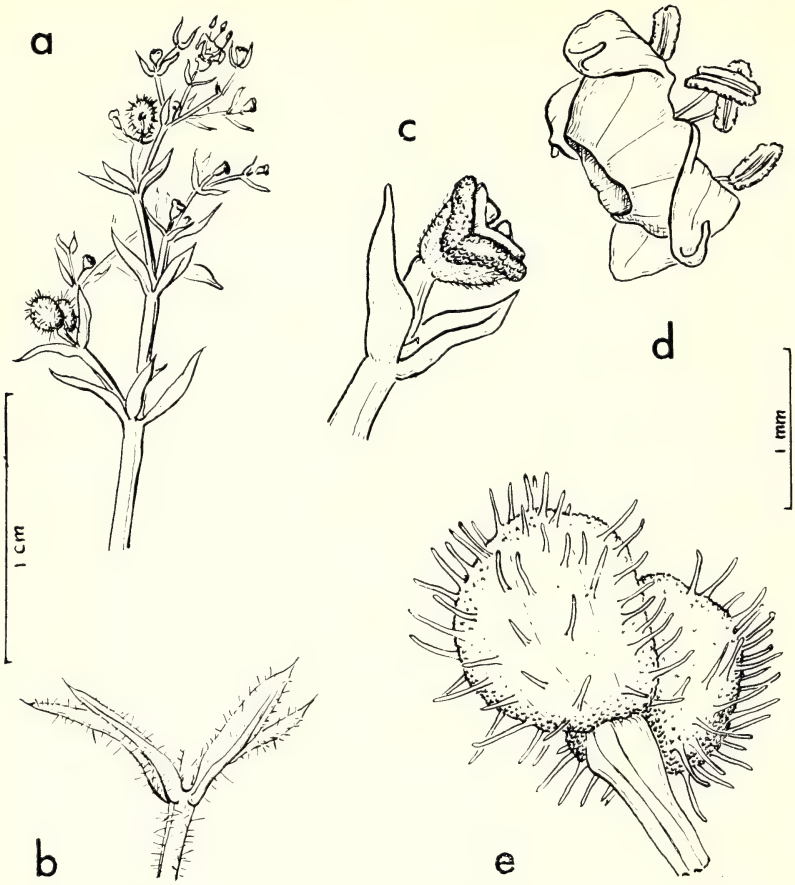

FIG. 1. *Galium carmenicola.* a, fertile branchlet with two fruits, one staminate flower, and eight sterile ovaries from which the corollas have fallen; b, node, showing leaves and indument; c, sterile ovary, pedicel, and subtending bracts of staminate flower; d, corolla and stamens of same; e, mature fruit.

hairs "straight" or somewhat curved, but a few so curved at the tip as to be necessarily described as uncinate, or at least uncinulate. Species that have uncinate fruit hairs (*G. aparine* L., *G. uncinulatum* DC., *G. proliferum* Gray, and many others) are usually unambivalent in this respect. Their fruit hairs are straight until the tip, which is suddenly hooked. On the other hand, although sect. *Lophogalium* Schum. is characterized by fruit hairs that are straight and not hooked, there are several species that must be included therein by reason of their obviously close relationship, but whose fruit hairs are clearly curved, rather than straight. Examples are *G. jepsonii* Hil. & How., *G. buxifolium* Greene, and many individuals of *G. fendleri* Gray. Apparently *G. carmenicola* belongs to this small group of aberrant members of the sect. *Lophogalium*.

I thank Rimo Bacigalupi for checking the Latin.

THE CALIFORNIA SPECIES OF ASPIDOTIS

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Wagner and Gilbert (1957) first described *Aspidotis carlotta-halliae* (Wagner & Gilbert) Lellinger, a rare endemic California fern from Mt. Tamalpais in Marin County. Because *A. carlotta-halliae* is morphologically intermediate between *A. densa* (Brack.) Lellinger [≡ *Cheilanthes siliquosa* Maxon] and *A. californica* (Hook.) Nutt. ex Copel. [≡ *Cheilanthes californica* (Hook.) Mett.] and produces larger spores than either, they hypothesized that it arose by allopolyploidy from a hybrid between the two latter species. Knobloch (1966) reported chromosome numbers of $2n = 30$ II for *A. densa* and *A. californica,* and a count of $2n = 30$ II + 30 I for a presumed backcross of *A. carlotta-halliae* to *A. californica.* The specific status and presumed origin of *A. carlotta-halliae* have not been universally accepted. Howell (1960) expressed doubt about the specific status of *A. carlotta-halliae* because of the variety of intermediates between *A. densa* and *A. californica* at the type locality. Hoover (1966, 1970) considered *A. carlotta-halliae* to be a mere sporadic variant of *A. densa* and reduced it to the status of forma under the latter species.

The diversity of opinions regarding the status of *A. carlotta-halliae* prompted a reinvestigation of its relationships to its postulated parents. All three Californian species were studied morphologically, cytologically, and chromatographically. Hybridization attempts have thus far been inconclusive and are not discussed here. Because of reported substrate preferences of the species, experiments were conducted to determine whether gametophytes differed in growth response on different soils. *Aspidotis densa* grows preferentially on soils derived from serpentine or other ultramafic rocks, not only in California but throughout its range (St. John, 1963; Kruckeberg, 1969). *Aspidotis carlotta-halliae* has been reported only on serpentine (Peñalosa, 1963). On the other hand, *A. californica* is found on soils derived from granitic rocks, or at least not serpentine. Notes from herbarium specimens and field observations substantiate these habitat preferences.

Following Lellinger (1968), I consider these species to belong to *Aspidotis,* a segregate of *Cheilanthes* comprising four North American species,

[1] This study was initiated as a seminar project under the direction of the author at the University of California, Berkeley, in Spring 1972. Participants were James E. Eckenwalder; Fred R. Ganders; Ann M. Hirsch; Dale E. Johnson; Stefan Kirchanski; George E. Pilz; W. Paul Sanders; M. Y. Sheikh; Dan B. Walker; Stephen G. Weller; and Pamela Yorks.

the three already mentioned and *A. meifolia* (D. C. Eaton) Pic.-Ser. from northeastern Mexico. *Aspidotis* is distinguished from *Cheilanthes* by elongate, narrow, generally mucronate-rostrate and distantly toothed frond segments, lack of indument on axes and laminae, striate and shining adaxial surface of laminae, and broad, scarious indusia.

Materials and Methods

Extensive field work was conducted throughout California to locate populations of *Aspidotis*. In addition, approximately 230 herbarium specimens of *A. densa*, 115 of *A. californica*, and 30 of *A. carlotta-halliae* were examined from CAS, DS, and UC. Measurements were made of characters suggested by Wagner and Gilbert (1957), except that basal pinna length was measured instead of blade width. Spore-diameter measurements were recorded for exospore only (perispore excluded).

Chromosome counts were made from sporogenous cells undergoing meiosis, or in a few instances from mitotic cells within sporangia. Fertile fronds were fixed in Carnoy's solution and preparations stained with aceto-carmine. Voucher specimens are in UC; voucher slides are in the author's collection.

Flavonoid chemistry was studied from dried fronds extracted in 0.5 percent HCl in methanol, using 2-dimensional descending paper chromatography with 3:1:1 (v:v:v) tert-butanol:acetic acid:water as the first solvent and 15 percent acetic acid as the second solvent. Collections used in constructing chromatographic profiles are indicated by an asterisk in Table 1. In addition, the following herbarium collections were studied chromatographically: *Howitt 1304* (CAS), *Howell* & *Leschke s.n.*, 1943 (CAS), and *Hardham 5647* (CAS), all *A. carlotta-halliae; Bacon s.n.*, 1902 (DS), *Saunders s.n.*, 1906 (CAS), *Howell 16925* (CAS), and *Quick 1824* (CAS), all *A. densa*.

Soil and spore samples for use in gametophyte growth studies were collected from the following localities:

1. *A. densa* population. Marin Co., slope above Alpine Lake on Fairfax-Bolinas Rd. Clay-loam soil overlying serpentine.
2. *A. carlotta-halliae* population *(Smith 575H, 2n* = 60 II). Marin Co., Mt. Tamalpais, below Bootjack Camp. Clay-loam soil overlying serpentine.
3. *A. californica* population *(Smith 561, 2n* = 30 II). Monterey Co., Pfeiffer Big Sur State Park, Pine Ridge Trail. Humus and decomposed granite.
4. *A. densa* popuation *(Smith 575E, 2n* = 30 II). Marin Co., Mt. Tamalpais, above Bootjack Camp. Serpentine-derived soil.
5. No *Aspidotis* present. Marin Co., Mt. Tamalpais, above Bootjack Camp. Pulverized serpentine rock.

For gametophyte growth studies, substrates were prepared by tamping a one-inch layer of sterilized soil over a two-inch layer of sterilized vermiculite in culture dishes. Dishes were watered with distilled water.

TABLE 1. CHROMOSOME NUMBERS IN ASPIDOTIS. Collections used in constructing chromatographic profiles are indicated by an asterisk.

Aspidotis californica (Hook.) Nutt. ex Copel. $2n = 30$ II, $2n = 60$ II.
DIPLOIDS: California: Fresno Co., 4.2 km (2.6 mi) N of State Hwy 180 on Elwood Rd, *Smith 636*; Fresno Co., ca 1.5 km (1 mi) S of Maxon Rd and Trimmer Springs Rd, *Smith 637*; Fresno Co., 12.3 km (7.6 mi) W of Big Creek along Trimmer Springs Rd, *Smith 839*; Los Angeles Co., San Gabriel Mts., Eaton Canyon, *Smith 557**; Monterey Co., Pfeiffer Big Sur State Park, Pine Ridge trail, *Smith 561**; San Diego Co., near Pala, *Fischer 4341**; San Diego Co., near Barrett Dam, *Harvey s.n.* [*Knobloch 63–5*] (MSC); Tulare Co., 6.6 km (4.1 mi) E of Springville on State Hwy 190, *Smith 624;* Tulare Co., 9.8 km (6.1 mi) E of Kaweah River along State Hwy 198, *Smith 628*; 11.3 km (7.0 mi) N of State Hwy 216 on J21, *Smith 635*.
TETRAPLOIDS: California: Amador Co., Lancha Plana Road, 1.3 km (0.8 mi) S of intersection with Comanche Parkway, *Smith 648*; Calaveras Co., 0.8 km (0.5 mi) N of Parrots Ferry Bridge, along road to Vallecito, *Smith 602*; El Dorado Co., 10.5 km (6.5 mi) N of Plymouth along State Hwy 49, *Smith 649*; Lake Co., 0.6 km (0.4 mi) W of State Hwy 175 on road to Anderson Springs, *Smith 653*; Marin Co., ca 3 km (2 mi) N of Alpine Lake Dam, *Smith 650*; Mariposa Co., 47.0 km (29.1 mi) NE of Mariposa along State Hwy 140, *Smith 642*; Napa Co., 4.8 km (3.0 mi) ENE of Napa along State Hwy 121, *Smith 658;* Tuolumne Co., Italian Bar, *Smith 599*; Tuolumne Co., 2.7 km (1.7 mi) E of Tuolumne Confidence Rd along Buchanan Rd, *Smith 645*; Tuolumne Co., 5.6 km (3.5 mi) N of Columbia on road to Vallecito, *Smith 646*.

Aspidotis carlotta-halliae (Wagner & Gilbert) Lellinger. $2n = 60$ II, $2n =$ ca 120.
California: Marin Co., Mt. Tamalpais, vicinity of Bootjack Camp, *Smith 575B**, *575D**, *575H, 607, 608, 609, 610, 614;* Marin Co., Bootjack, *Roderick s.n.** [UC Botanical Garden Acc. 62.039]; Monterey Co., Los Padres National Forest, ca 1.5 km (1 mi) downstream from Alder Creek Campground, *Smith 579**, *580, 582, 583, 584, 586, 587, 588, 593, 595, 596, 597*.

Aspidotis densa (Brack.) Lellinger. $2n = 30$ II.
California: Humboldt Co., ca 8 km (5 mi) S of Somes Bar on State Hwy 96, *Smith 572**; Lake Co., 1.8 km (1.1 mi) W of Napa Co. line on Butts Canyon Rd, *Smith 654*; Marin Co., Mt. Tamalpais, along Old Stage Road above Bootjack Camp, *Smith 575C, 575E*; Napa Co., 0.3 km (0.2 mi) N of State Hwy 128 along Berryessa-Knoxville Rd., *Smith 657;* Siskiyou Co., Scott Mt. Rd., ca 6.5 km (4 mi) SE of intersection with road to Callahan, *Smith 570*; Siskiyou Co., ca 8 km (5 mi) E of Somes Bar on State Hwy 96, *Smith 573*; Tuolumne Co., N side of Hetch Hetchy Reservoir, *Yorks 101*. Cultivated plant, *Knobloch 63–9* (MSC).

Aspidotis meifolia (D.C. Eaton in Wats.) Pic.-Ser. $2n = 30$ II.
Mexico: Tamaulipas, W of Victoria, *Knobloch 2251* [UC Botanical Garden Acc. 68.244].

Aspidotis californica × *carlotta-halliae*. $2n = 30$ II + 30 I.
Monterey Co., vicinity of Alder Creek, *Kiefer 1358* (MSC).

Controls were grown on one percent nutrient agar using modified Prague's medium. Spores were suspended in distilled water and about 150 spores delivered to each dish. Number of spores delivered per dish was determined by counting spores in sample aliquots. Culture dishes were placed in a growth chamber, temperature 17°C, fluorescent lights, 350 f.c., photoperiod 16/8 (light/dark).

Results

Morphology (data collected by D. E. Johnson, G. E. Pilz). Morphological studies confirm those of Wagner and Gilbert (1957) in that they show similar directions and magnitudes of differences among the three taxa. *Aspidotis carlotta-halliae* tends to be intermediate between *A. densa* and *A. californica* in all characters examined except petiole length and petiole/blade length ratio. Our data, since they support previous data, are not reproduced here, but are on file with chromosome vouchers in UC.

Relative degree of dissection of indusia in mature fronds appears to be the best single character for separating the taxa, since there is considerable overlap among taxa for other characteristics. Sterile (usually juvenile or early season) fronds of *A. densa* are often more dissected than mature fertile fronds; partially fertile fronds often show more dissection of indusia than do fully fertile fronds, and so may be mistaken for *A. carlotta-halliae*. Nearly all collections identified as forma *carlotta-halliae* by Hoover (1966, 1970) are juvenile, sparingly fertile specimens of *A. densa*. Similarly, juvenile fronds of *A. carlotta-halliae* are more dissected than adult fronds of the same species and may consequently be mistaken for *A. californica*.

Cytology (data collected by A. R. Smith, S. G. Weller). Chromosome counts for *Aspidotis* are listed in Table 1; three previous counts by Knobloch (1966) are indicated by location of the voucher (MSC). These counts show that *A. carlotta-halliae* is indeed polyploid ($2n = 60$ II), as predicted by Wagner and Gilbert (1957). All counts of *A. densa* are diploid ($2n = 30$ II).

Unexpectedly, *A. californica* proved to consist of both diploid and tetraploid cytotypes (Table 1). Diploid plants occur in the Coast Ranges from Monterey Co. to San Diego Co. and also in the foothills of the Sierra Nevada from Kern Co. to Tuolumne Co.; tetraploids occupy the northern half of the distribution of *A. californica,* occurring in the North Coast Ranges from Marin Co. to Mendocino Co. and in the Sierra Nevada foothills from Mariposa Co. to Butte Co. Figure 1 illustrates the distribution of the two cytotypes as judged from both chromosome counts and spore measurements. There is a narrow area of apparent sympatry—apparent because the two cytotypes have not yet been found growing together—in Tuolumne and Mariposa counties. In the Sierra Nevada, the two cytotypes are very similar morphologically, but tetraploids are generally more robust and thicker-textured than diploids, and spore diameter in the tetraploids is larger. However, small-spored diploids from southern California attain or even surpass the Sierra Nevada tetraploids in robustness.

Spore morphology (data collected by M. Y. Sheikh). Because relative spore size is often useful in predicting ploid among closely related species, we measured spore diameter in *Aspidotis* (Table 2). Wagner and Gilbert (1957) found that spores of *A. carlotta-halliae* were larger than spores of either *A. densa* or *A. californica*. Our measurements confirm

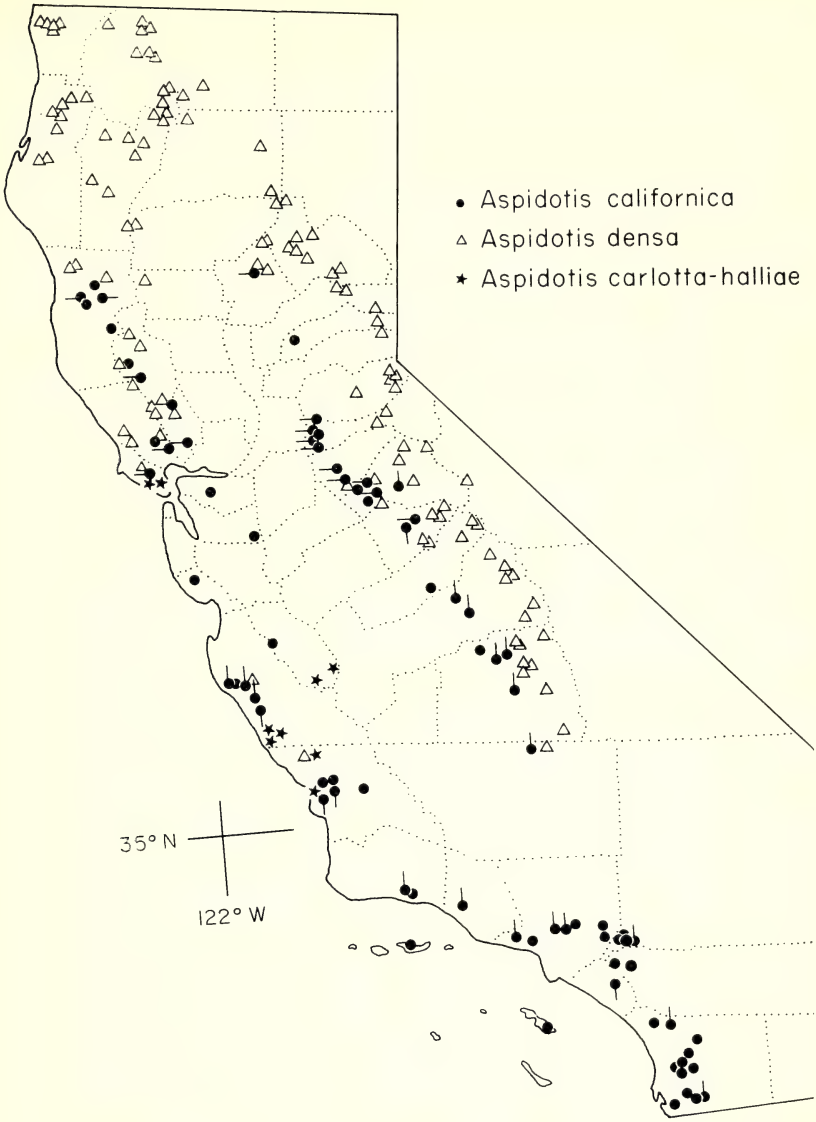

FIG. 1. Distribution of *Aspidotis* in California. Symbols with vertical rays indicate collections known to be diploid from chromosome counts or judged to be diploid from spore measurements. Symbols with horizontal rays indicate collections known to be tetraploid from chromosome counts or judged to be tetraploid from spore measurements.

this only when suspected diploids of *A. californica* are considered, but known tetraploids of *A. californica* (e.g., *Smith 602;* spores 46–59 μm, mean 52 μm) have spores similar in size to spores of *A. carlotta-halliae*

TABLE 2. SPORE DIAMETERS IN ASPIDOTIS SPP. Mature spore and meiotic stages are rarely present in single plants at the same time; both chromosome number and spore size are available for only one plant (cited in text). Ploidal levels (number of populations sampled given in parentheses) are summarized from data in Table 1. N = number of specimens sampled. Ten spores were measured for each specimen.

Taxon	N	Range of sample means, μm	Absolute range, μm
A. densa, 2*x* (8) (California)	10	39–45	35–49
A. carlotta-halliae, 4*x* (2) (California)	10	48–58	42–64
A. californica, 2*x* (4) (Coast Ranges, Monterey Co. to San Diego Co.)	10	39–44	30–48
A. californica, 2*x* (6) (Sierra Nevada, Tuolumne Co. to Kern Co.)	6	40–44	37–48
A. californica, 4*x* (10) (Sierra Nevada, Butte Co. to Mariposa Co.; N Coast Ranges)	10	47–51	42–60

(Table 2). Sporangial size, length and width of spore laesurae, and perispore thickness all are correlated to some extent with spore size, being larger or thicker in *A. carlotta-halliae* and tetraploid *A. californica* than in diploid *A. californica* or *A. densa*. Additionally, there are subtle differences in spore ornamentation among species of *Aspidotis*. The perispore in *A. californica* and *A. carlotta-halliae* is somewhat more fimbriate than in *A. densa* but less fimbriate than in *A. meifolia*.

Flavonoid chemistry (data collected by J. E. Eckenwalder). Considerable chromatographic variation occurs among populations of the same species. Nevertheless, except for some anomalous specimens of *A. californica* from southern California, chromatograms of both *A. densa* and *A. californica* possess characteristic spots, shown in the composite chromatogram (fig. 2). Most importantly, chromatograms of *A. carlotta-halliae* showed characteristic spots of both *A. densa* and *A. californica*. Spots 7, 9, and 27 were present in nearly all collections of *Aspidotis;* spots 24, 25, and 35 were present in *A. densa* and *A. carlotta-halliae,* but absent in *A. californica;* and spot 12 was present in *A. californica* and *A. carlotta-halliae,* but absent in *A. densa*. Two additional spots, 13 and 32, were often absent in *A. densa*, but present in *A. californica* and *A. carlotta-halliae*. Tetraploid material of *A. californica* has not yet been tested chromatographically.

Gametophytes (data collected by D. Walker, W. P. Sanders, and F. Ganders). Gametophyte growth on different natural soils was determined after 18 weeks. Gametophytes were counted, and spore germination percentages for each species on each soil are given in Table 3 (one standard deviation given for number of spores plated and percent germination). All species showed greater than 75 percent germination on

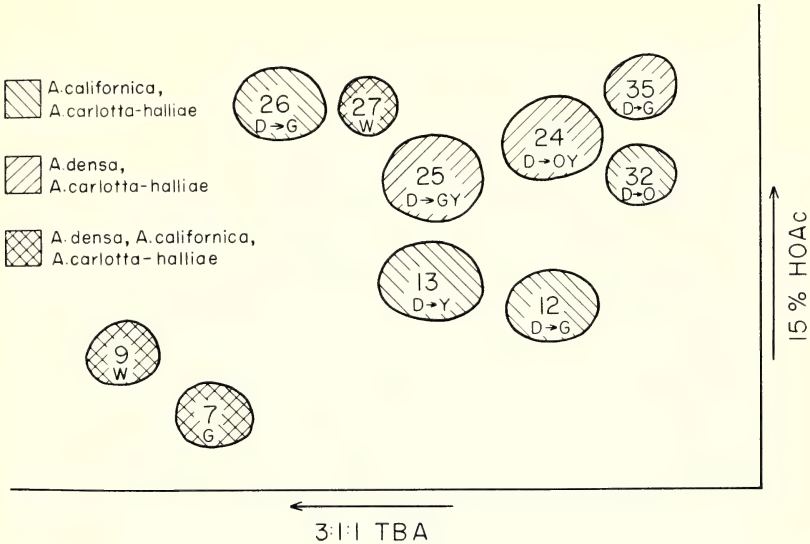

FIG. 2. Composite chromatogram of *Aspidotis* spp. in California. Color reactions under UV light are given beneath spot number: B = Blue; G = Green; O = Orange; W = White; Y = Yellow; D = Absorbing. Arrows point to color change when viewed under UV + NH_3. Spots 13 and 32 were infrequently present on chromatograms of *A. densa*.

agar, indicating high spore viability. With few exceptions, *A. densa* spores showed the highest germination percentages on all soils, *A. californica* was next, and *A. carlotta-halliae* the lowest. In general, spore germination percentages in all species were correlated with particle size of the soil, germination and growth being favored by smaller-particled substrates such as the clay-loam soils. This is probably related to the water-holding capacity of the soils, which is inversely proportional to particle size.

The data show no correlation between spore germination and the soil on which sporophytes are found. The virtual absence of germination and growth on pure serpentine rock is probably due to its poor water-holding capacity but could be due to inhibition by some chemical factor. Gametophyte requirements do not appear to be responsible for the edaphic preferences exhibited by sporophytes in nature. Other factors, such as moisture, competition, and sporophytic requirements must restrict these ferns to their respective habitats.

Number of spores per sporangium is consistently 64 for all four species of *Aspidotis*, suggesting that they are sexual and that apogamy is not a typical feature of their life cycle, as it is in many cheilanthoid ferns. Gametophytes of all species are initially female and later become hermaphroditic. Development of archegonia before antheridia is supposedly uncommon in fern gametophytes, but is the normal sequence in

TABLE 3. SPORE GERMINATION OF ASPIDOTIS SPP. ON VARIOUS SUBSTRATES. Numbers preceding species names refer to populations from which spores and substrate were obtained (see Materials and Methods). Percent germination is included parenthetically after number of spores germinated.

Substrate source	1. *A. densa* 150 ± 14.8 spores plated	3. *A. californica* 142 ± 8.5 plated	2. *A. carlotta-halliae* 144 ± 8.4 plated
Nutrient agar	122 (81.4 ± 7.3)	164[a] (115.2 ± 6.2)	109 (75.8 ± 4.3)
1. *A. densa;* clay-loam	138 (92.0 ± 8.1)	109 (76.7 ± 4.2)	94 (65.3 ± 3.7)
2. *A. carlotta-halliae;* clay-loam	128 (85.4 ± 7.6)	124 (87.2 ± 4.7)	89 (61.8 ± 3.4)
4. *A. densa;* serpentine-derived soil	82 (54.6 ± 4.8)	60 (42.2 ± 2.3)	77 (53.5 ± 3.0)
3. *A. californica;* humus decomposed granite	73 (48.6 ± 4.3)	50 (35.2 ± 2.0)	38 (26.4 ± 1.5)
5. No *Aspidotis*; crushed serpentine rock	1 (0. ± 0.1)	0 (0.)	0 (0.)

[a] Higher than expected germination probably due to clumping of spores at time of plating, as evidenced by a few clumps of gametophytes. Clumping was ordinarily not a problem, with gametophytes distributed more or less randomly.

Aspidotis, many Blechnaceae (Klekowski, 1969b), and several other ferns. This has been interpreted as an adaptation for outcrossing (Klekowski, 1969a).

DISCUSSION AND CONCLUSION

Aspidotis carlotta-halliae is morphologically intermediate between *A. densa* and *A. californica,* shows additive flavonoid chemistry, and is a fertile, sexual tetraploid. It shows slightly lower spore germination percentages than its diploid relatives. Tetraploids derived from diploid hybrids often show reduced fertility (Stebbins, 1950). Gametophytes of all three Californian species are capable of growth on serpentine or non-serpentine soils in laboratory cultures. These gametophytes develop sex organs in a sequence that is thought to promote intergametophytic mating.

The alleged backcross reported by Knobloch (1966) remains enigmatic. The voucher *(Kiefer 1358,* Knobloch Acc. 64–20, MSU!) is a typical specimen of *A. carlotta-halliae.* I have reexamined voucher slides prepared by Knobloch and also slides made by Wagner from plants of the same collection *(Kiefer 1358,* MICH!) and concur that the chromosome complement of cells at meiosis is ca 30 II + 30 I. I have also revisited the locality in question and obtained chromosome counts from thirteen plants throughout the population. All plants showed unequivocally either $2n = 60$ II, with normal pairing behavior at meiosis, or $2n = 120$ in somatic cells (Table 1). Neither *A. californica* nor *A. densa* could be found in the immediate area, although they certainly could occur there (or might have occurred in the past). One explana-

tion for these seemingly disparate facts is that the chromosome voucher at MSU may not be the plant actually counted—that within the original gathering by Kiefer there were both *A. carlotta-halliae* and the backcross to *A. californica*. In support of this hypothesis is the fact that another collection of *Kiefer 1358* at MSU (!) seems more likely to be a backcross. Alternatively, the backcross could be morphologically so like *A. carlotta-halliae* that the two would be indistinguishable without cytological or palynological data.

The distribution of *A. carlotta-halliae* is rather limited, with a much smaller range than either of its presumed parent species. Wagner and Gilbert (1957) recorded it from three counties in the Coast Ranges: Marin, San Benito, and San Luis Obispo. It is now known from several stations in Monterey Co. and from additional localities in all of the first three counties (fig. 1). At the type locality, Bootjack Camp, Marin Co., there is a large population of *A. carlotta-halliae,* but, contrary to Howell (1960), neither *A. densa* nor *A. californica* could be found in this population. *Aspidotis densa* is abundant nearby in chaparral and on serpentine above Bootjack Camp and actually grows with *A. carlotta-halliae* along a narrow interface between chaparral and woodland. This is the only area where I know of two species of *Aspidotis* growing together. Hybrids have not yet been found along this interface. *Aspidotis californica* is apparently much rarer in Marin Co., where it was found growing at the bases of decomposing granitic boulders. It is probable that in the Coast Ranges edaphic preferences prevent all but rare contact between *A. densa* (on serpentine) and *A. californica* (on non-serpentine). In the Sierra Nevada, elevational differences separate the two species, with *A. densa* occurring at higher elevations (on or off of serpentine). *Aspidotis californica* has not yet been found growing with either *A. densa* or *A. carlotta-halliae*. The two cytotypes of *A. californica* occupy similar habitats, but tetraploids have seemingly adapted to a greater variety of situations (e.g., wet, rocky gullies and heavily shaded woodlands, as well as rocky outcrops) than have diploids.

Present distributions of the Californian species (fig. 1) show two areas where all three species occur and where the allotetraploid *A. carlotta-halliae* might have evolved: northern San Luis Obispo Co.-southern Monterey Co., and Marin Co. Since the diploid cytotype of *A. californica* is thus far unknown from Marin Co., one suspects that the origin of *A. carlotta-halliae* may have been in the first-mentioned area. Less certain is the origin of tetraploid *A. californica*. The two cytotypes of *A. californica* are close enough morphologically to suggest that autopolyploidy has occurred. There are slight differences in size and texture of fronds, especially in the Sierra Nevada, but there seems to be little basis for taxonomic recognition of the cytotypes other than perhaps as geographical varieties. No one, heretofore, has recognized discontinuity within *A. californica*. Additional chemical study seems the best avenue for shedding light on the origin of the tetraploid cytotype.

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TAXONOMY OF PSATHYROTES (COMPOSITAE: SENECIONEAE)

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Psathyrotes comprises five species of humble herbs, two in the Chihuahuan Desert and three in the Sonoran Desert and southwestern Great Basin. They typically grow in dry, sandy washes, among sand dunes, or on gravelly benches and alluvial fans. Economically these plants are are of no known consequence; aesthetically they are not particularly appealing. They have received little attention from botanists other than compilers of regional floras and, therefore, have been relatively poorly known. Heretofore, morphological circumscriptions of at least two species and geographic ranges of three have been confusedly or inaccurately delineated in regional and local floras. We hope that our observations will serve to abrogate the confusion and to redress the inaccuracies.

A brief chronology of the taxonomic history of the genus follows:

1848. Nuttall described the first plant to be assigned to the genus, *Bulbostylis annua,* placing it in a monotypic section, *Psathyrotus* [sic]. (*Bulbostylis* DC. is now generally considered to be a synonym of *Brickellia* Ell., a member of Eupatorieae.) Later in the same year, Torrey named a new species, *Tetradymia ramosissima,* placing it in a new, monotypic subg. *Polydemia.* (*Tetradymia* is a member of Senecioneae.)

1853. Gray altered the rank of Nuttall's section to genus, corrected the orthography to *Psathyrotes,* and added a second species (*P. scaposa*), indicating that the genus should be "provisionally referred, I think, to Senecionideae of the subtribe Senecioneae". He did not mention *Tetradymia ramosissima.*

1854. Gray described *Psathyrotes incisa* as a third species of the genus. At the same time, Gray said that Torrey had informed him that *Tetradymia ramosissima* and *P. annua* refer to the same species and asserted that Torrey "had rightly indicated the affinities of the plant" (i.e., with *Tetradymia*).

1859. Gray (Bot. Mex. Bound.) transferred *P. incisa* to a new, monotypic genus, *Trichoptilium,* in Helenieae, commenting that Torrey had "pointed out the oversight I [Gray] had committed in respect to the pappus, and which led me wrongly to refer the plant to Psathyrotes".

1868. Without compromising Torrey, Gray acknowledged that he (Gray) "had confounded" *P. annua* with "a related but distinct species", *Tetradymia ramosissima,* which he transferred to *Psathyrotes.* He treated these two species as belonging to one section and *P. scaposa* as belonging to a second. Both sections were carefully diagnosed but neither was formally named.

1873. Bentham (in *Genera plantarum*) listed *Trichoptilium* and *Psathyrotes* at the end of Helenieae, remarking that, while the pappus of *Psathyrotes* is close to that of Senecioneae, other characters seem to indicate affinity with Helenieae. He also indicated that whether the pappus of *Trichoptilium* is interpreted as bristles or fimbriate paleae, it is nevertheless similar to that of *Psathyrotes* (see also Bentham, 1873, p. 449).

1874. Gray, partly in response to Bentham, stated that *Psathyrotes* belongs in Senecioneae close to *Luina* Benth. and *Tetradymia.* He indicated that *Trichoptilium* might also belong in Senecioneae. Additionally, he transferred *Peucephyllum* A. Gray (a monotype, *P. schottii,* originally referred to Eupatorieae by Gray but included in Senecioneae next to *Luina* by Bentham) to *Psathyrotes* as a distinct section.

1880. Gray briefly characterized a new species, *P. pilifera,* and indicated its close affinity to *P. annua* and *P. ramosissima.*

1884. In the *Synoptical flora,* Gray maintained *Psathyrotes* in Senecioneae, referring *P. annua, P. pilifera,* and *P. ramosissima* to one section and *P. scaposa* to a second (both still nameless). He returned *P. schottii* to *Peucephyllum* without comment.

1889. In his treatment for Compositae for *Die natürlichen Pflanzenfamilien,* Hoffmann referred *Psathyrotes* (with four species) to Senecioneae without comment.

1911. Brandegee described *P. purpusii,* stating that it "is a very distinct species" and "perhaps it should be considered the type of a genus".

1927. Rydberg, in the last comprehensive treatment of these plants (in N. Amer. Fl.), segregated Brandegee's species to a monotype,

Psathyrotopsis, wrongly stating that the tube of the corolla equals the throat. He also segregated *P. scaposa* to a monotype, *Pseudobartlettia.* The other species *(P. annua, P. pilifera,* and *P. ramosissima)* were retained in *Psathyrotes.* These three "genera" were grouped together in his subtribe "Senecionanae". He placed *Peucephyllum* in his subtribe "Luinanae", commenting that it "is an abnormal genus" in Senecioneae "and probably should be transferred to Astereae, next to *Ericameria*".

Generic Relationships

Cronquist (1955), Powell and Turner (1974), and others have remarked the heterogeneity and artificiality of Helenieae and have suggested that most genera historically assigned to this dust bin of a tribe would be better placed in Heliantheae or Senecioneae. In particular, Cronquist (1960) said, "*Psathyrotes, Peucephyllum* and some other small southwestern genera have customarily been excluded from Heliantheae (Helenieae) because of their capillary pappus, and referred to the Senecioneae instead. Their relationship to the main bulk of the Senecioneae is doubtful, however, and further investigation of the affinities of these genera is well warranted." Actually, among *Psathyrotes* only *P. pilifera* has a truly capillary pappus (in other species the bristles are rather coarse) and in southernmost colonies of *Peucephyllum* the pappus consists of well developed squamellae subtended by coarse bristles. Cronquist (1955) suggested the "origin of a capillary pappus by longitudinal fission of the scales" and proposed that steps in such a development are illustrated by several genera including *Dyssodia.* Strother (1969) indicated, however, that the simple squamellate pappus in *Dyssodia* is a derived condition and that the primitive pappus in the genus consists of squamellae formed of basally coalesced bristles.

In spite of these contradictory interpretations of pappus, there seems little doubt that *Psathyrotes* and *Peucephyllum* are closely related. The two are very similar in details of corollas, style branches, anthers, and achenes. The branching pattern of robust, suffrutescent plants of *P. ramosissima* is quite like that of *Peucephyllum,* although the latter is decidedly shrubby and has distinctive foliage. Carlquist (1962) included *Peucephyllum* in his survey of wood anatomy in Senecioneae and concluded that the wood is highly specialized but affords no character expressions suggesting a particular taxonomic placement. In their survey of pollen ultrastructure in Compositae, Skvarla and Turner (1966) assigned pollen of *Psathyrotes annua* to their Helianthoid-type and pollen of *Peucephyllum* to their Senecioid-type. Meiotic chromosome morphology and chromosome numbers are similar in *Psathyrotes* ($x = 19, 17$) and *Peucephyllum* ($x = 20$). Collectively, these data encourage recognition of separate but closely related genera.

Historically, as outlined above, these genera have been associated with *Trichoptilium* A. Gray, *Tetradymia* DC., and *Luina* Benth. The similarity between *Psathyrotes* and *Trichoptilium* ($x = 13$) is wholly

superficial; the relationship between them is remote. *Trichoptilium* is probably best placed in Eriophyllinae. *Tetradymia* ($x = 30$), *Luina* ($x = 30$) and a few other genera form a distinct alliance within Senecioneae (Strother, 1974) but are not closely related to *Psathyrotes* and *Peucephyllum*.

Where, then, did *Psathyrotes* come from? We still don't know. Careful postulation of an archetype combining putatively primitive character states for members of the genus allows development of a reasonable answer. Despite warnings of possible typological entrapment (Davis and Heywood, 1963), this seems an acceptable approach for determining affinities in many groups of Compositae, since several trends of specialization within the family are fairly well documented (Cronquist, 1955).

An archetype for *Psathyrotes* would have been a perennial, perhaps suffrutescent, herb with alternate, laminar, probably woolly, leaves, a simple capitulescence, a 2–3-seriate involucre of scarcely differentiated phyllaries, many (ca 50?) florets in each head, disc corollas with short tubes and lobes and relatively long, cylindrical throats, sagittate anthers, weakly appendaged, papillate style branches, and pyramidal achenes supporting a coarsely setose, 2–4-seriate pappus. Using this hypothetical but reasonable characterization of an ancestor for *Psathyrotes* as a basis for comparison, several aspects of morphology (e.g., habit, indument, involucre, corollas, style branches, and anthers) suggest *Hulsea* Torr. & Gray as a possible relative. *Hulsea* comprises about ten species of perennial or annual herbs that grow at middle to high elevations in western North America, especially in the drier mountains of the southwestern Great Basin and northwestern Sonoran Desert. Skvarla and Turner (1966) assigned pollen of *Hulsea carnosa* Rydb. to their Helianthoid-type. Cytological evidence supports morphological arguments for propinquity, since the chromosome base number of *Hulsea* ($x = 19$) is the same as that of primitive species of *Psathyrotes* (see below). Members of both genera are strongly scented with balsamic or turpentine odors, perhaps reflecting underlying chemical similarities.

Traditionally, *Hulsea* has been assigned to Helenieae. In 1962, Turner suggested a possible alliance to Senecioneae. Ornduff et al. (1967) agreed and indicated that both *Hulsea* and *Whitneya* ($n = 38$) belong in Senecioneae near *Arnica* ($x = 19$). Powell and Turner (1974) recently presented arguments for transferring several genera (Perityllinae, including *Hulsea*) from Helenieae to Senecioneae. They said that *Hulsea* might be "viewed as a possible ancestral prototype" for Perityllinae. While derivation of *Psathyrotes* and *Peucephyllum* from extant members of *Hulsea* seems unlikely, an hypothesis that these three genera derived from a fairly immediate common ancestor does seem reasonable. We do not feel, however, that *Psathyrotes* or *Peucephyllum* should be added to Perityllinae sensu Powell and Turner but rather that they belong to a separate, related group for which we are not yet prepared to offer a circumscription.

Chromosomes and Species Relationships

We have studied chromosomes in four species of *Psathyrotes* and chromosome numbers are now known for all five species of the genus (Table 1). Our observations were made from standard aceto-carmine

Table 1. Chromosome Counts for Psathyrotes. Pilz and Strother are abbreviated *P* and *S*, respectively, in citing collections; our vouchers are in UC. Our counts are reported as meiotic pairing configurations at diakinesis or early first metaphase. Parenthetical numbers refer to numbers of individuals examined.

Psathyrotes annua (Nutt.) A. Gray

CA, Inyo Co., ca 15 mi E Keeler, *P 1223,* **17 II;** 4 mi N Darwin, *Kyhos 58–196* (JEPS), **17 II** (reported as *P. ramosissima,* Ornduff et al., 1963).

CA, Kern Co., Red Rock Canyon, *Hill 47871–G* (DS), **17/17** at first anaphase (unpublished).

NV, Clark Co., 3 mi E Indian Springs, *P 1185,* **17 II.**

NV, Esmeralda Co., 22 mi W Tonopah, *P 858,* **17 II;** 7 mi S Goldfield, *Spellenberg 2107* (NY), **17 II** (Spellenberg, 1971a; 1971b).

NV, Lincoln Co., 12 mi S Alamo, *P 813,* **17 II;** 4 mi W Crystal Springs, *P 817,* **17 II.**

NV, Mineral Co., near Basalt, *P 854,* **17 II.**

NV, Nye Co., 16 mi W Lockes, *P 859,* **17 II plus 1—3 B.**

NV, Pershing Co., 15 mi S Lovelock, *P 729,* **17 II.**

NV, Washoe Co., 12 mi NW Nixon, *P 738* and *739,* **17 II;** W edge Winnemucca Dry Lake, *Ornduff 4202* (UC), **17 II** (Ornduff et al., 1963).

UT, Washington Co., 4 mi NE St. George, *P 821,* **17 II.**

Psathyrotes ramosissima (Torr.) A. Gray

[Note: Voucher *(Kyhos 58–196)* for a report for this taxon by Ornduff et al. (1963) is *P. annua.*]

AR, Yuma Co., 31 km W county line on Interstate Rte. 10, *S 1220,* **17 II** (3).

CA, Inyo Co., ca 7 mi W Townes Pass, *P 1224,* **17 plus 2 B;** just E Tecopa Pass, *S 1215,* **17 II;** ca 4.8 km N county line on road from Trona to Panamint Valley, *S 1218,* **17 II** (5), **17 II plus 3 B** (1); Death Valley, near Ubehebe Crater, *Powell and Patterson 1611* (TEX), $n = 17$ (unpublished).

CA, Riverside Co., ca 9.5 km E Mecca, *S 1211,* **17 II** (3); ca 16 km E Mecca, *S 1212,* **17 II** (1), **17 II plus 0—3 B** (1), **17 II plus 6 B** (1); Palm Desert, *S 1213,* **17 II** (3); Chiriaco Summit, ca 48 km E Indio, *S 1219,* **17 II** (2), **17 II** or **15 II plus 1 IV** (1).

CA, San Bernardino Co., Rte. 127, just S Ibex Pass, *S 1216,* **17 II** (2); Rte 127, ca 19 km S Ibex Pass, *P 979,* **17 II;** *S 1199,* **17 II plus 0—1 B;** *S 1217,* **17 II** (3).

Psathyrotes pilifera A. Gray

UT, Washington Co., ca 3.2 km E LaVerkin, *S 1202,* **17 II** (4).

Psathyrotes scaposa A. Gray

Chihuahua, 20 mi W Ojinaga, *Powell, Turner, and Sikes 2468* (TEX), $n = 19$ (unpublished).

TX, Brewster Co., Terlingua, *Turner and Ellison 4598* (TEX), $n = 19$ (Turner and Ellison, 1960).

TX, Hudspeth Co., 12 mi W Sierra Blanca, *Powell and Averett 1487* (TEX), $n = 19$ (Powell and Sikes, 1970); 14 mi W Sierra Blanca, *Sikes 459* (SRSC), $n = 19$ (unpublished); 22 mi S Tommy's Town, *Powell 2420* (SRSC), $n = 19$ (unpublished).

TX, Presidio Co., 5.2 mi N Lajitas, *Powell 2391* (SRSC), $n = 19$ (unpublished).

Psathyrotes purpusii Brandeg.

Coahuila, ca 100 km W Saltillo (type locality), *P 715,* **19 II.**

squashes of pollen mother cells that were field-fixed in Carnoy's fluid. Meiosis seemed to be normal in the majority of preparations.

In four colonies of *P. ramosissima* and in one colony of *P. annua,* B-chromosomes were present in some plants. Most colonies for which more than one plant was studied were heterogeneous with respect to presence of B-chromosomes. During meiosis, the B-chromosomes usually behaved as univalents (rarely there was a tendency to associate in pairs), segregated randomly at first anaphase, and divided (usually early) at second anaphase. No laggards were observed; no micronuclei were present in tetrads. Pollen stainability (N = 200, lacto-phenol : cotton blue) ranges from 90 to 98 percent in plants with B-chromosomes and from 72 to 100 percent in plants lacking B-chromosomes. Geographic distribution of plants with B-chromsomes does not suggest a pattern. At present, we can offer no explanation for, nor can we assign any significance to, the occasional presence of B-chromosomes in *Psathyrotes.*

In one plant of *P. ramosissima,* the modal meiotic configuration was 15 II + 1 IV (see Table 1). Whether such translocation heterozygosity has contributed to occurrence of B-chromosomes in *Psathyrotes,* we cannot say.

Species of *Psathyrotes* form two morphologically and geographically natural groups. These groups are also distinct cytologically. The Chihuahuan Desert species have $x = 19$ and the Sonoran Desert-Great Basin species have $x = 17$. Morphologically, the Chihuahuan taxa are less specialized than the Sonoran-Great Basin group. It is reasonable, then, to postulate a dysploid reduction from a Chihuahuan ancestral type to a Sonoran-Great Basin ancestral type.

Of the Chihuahuan pair, *P. purpusii* is more primitive than *P. scaposa,* but each has distinctive, specialized traits indicating a relatively remote divergence from a common ancestor. In the Sonoran-Great Basin trio, *P. annua* seems to represent a northern facies fairly recently derived from *P. ramosissima* or a very recent common ancestor. These two species show occasional, local morphological intergradation where their ranges overlap (see Taxonomic Treatment). *Psathyrotes pilifera* is exceptionally specialized in several morphological traits (e.g., entire leaf margins, multicellular hairs of the herbage, reduced number of florets, capillary pappus, and ribbed achenes). It is closely but obscurely related to the other Sonoran-Great Basin species.

Taxonomic Treatment

Psathyrotes (Nutt.) A. Gray, Smithsonian Contr. Knowl. 5(6):100. 1853. — *Bulbostylis* DC. sect. *Psathyrotus* [sic] Nutt., Proc. Acad. Nat. Sci. Philadelphia 4:22. 1848. Type: *Bulbostylis annua* Nutt.

Tetradymia DC. subg. *Polydemia* Torr., *In* Emory, Notes Mil. Rec. 145. 1848. Type: *Tetradymia ramosissima* Torr.

Psathyrotopsis Rydb., N. Amer. Fl. 34:360. 1927. Type: *Psathyrotes purpusii* Brandeg.

Pseudobartlettia Rydb., N. Amer. Fl. 34:358. 1927. Type: *Psathyrotes scaposa* A. Gray.

Annual or perennial herbs or, rarely, subshrubs. Leaves alternate; petioled; laminar; round-deltoid to suborbicular or reniform; toothed, crenulate, or entire; loosely floccose-tomentose to lanate and/or furfuraceous but not glabrous. Capitulescence monocephalic or a subumbellate or corymbiform cluster of a few heads. Involucres cylindro-turbinate to hemispheric. Phyllaries several (8–24) in 2–3 similar or distinct series. Receptacle flat to convex; smooth to foveolate; glabrous to weakly hispid. Heads discoid; few (9) to several or many (50) flowered. Corollas pale cream to bright yellow, often tipped with red or purple; tube much shorter than the cylindrical throat; lobes 5, short, erect, deltoid, internally papillate, externally stipitate-glandular with bulbous-tipped hairs and often conspicuously to sparsely villous with slender, multicellular hairs. Anthers acute to blunt at apex; weakly to decidedly sagittate at base. Style branches weakly- to shaggy-papillate; rounded-truncate or weakly subulate-appendaged. Achenes cylindrical to obpyramidal; subscabrous to densely hirsute. Pappus of many to numerous, coarse to fine bristles in 1–4 series. Figure 1, a–e.

Key to *Psathyrotes*

1. Leaves cauline, at least somewhat furfuraceous (often tomentose as well); phyllaries clearly of two dissimilar series, at least the inner, chartaceous ones deciduous; Sonoran Desert and Great Basin. . 2.
1. Leaves mostly basal, loosely floccose to lanate but not furfuraceous; phyllaries obscurely of 2–3 similar series, all herbaceous and persistent; Chihuahuan Desert. . . . . 4.

2. Margins of all leaves entire, margins and veins conspicuously ciliate below with long, straight, multicellular hairs; achenes subscabrid, 4–5 mm long. . . . . 3. *P. pilifera.*
2. Margins of at least some leaves toothed, not ciliate with multicellular hairs; achenes densely hirsute, less than 3.5 mm long. . . . . 3.

3. Leaves weakly tomentose and furfuraceous; outer phyllaries erect, apices mostly lance-linear; florets 13–16 (10–20) per head; pappus of 35–50 bristles in one series. . . . . 1. *P. annua.*
3. Leaves velvety lanate and furfuraceous; outer phyllaries apically squarrose to reflexed, apices spatulate to obovate; florets 21–26 (16–32) per head; pappus of 120–140 bristles in 3–4 series. . . . . 2. *P. ramosissima.*

4. Heads borne in corymbiform clusters on branched, scapiform, glandular-puberulent stems; involucres broadly campanulate to hemispheric; phyllaries 4–6 mm long. . . . . 4. *P. scaposa.*
4. Heads borne singly or in subumbellate clusters on rather short, stout, woolly peduncles; involucres narrowly to broadly turbinate; phyllaries 9–10 mm long. . . . . 5. *P. purpusii.*

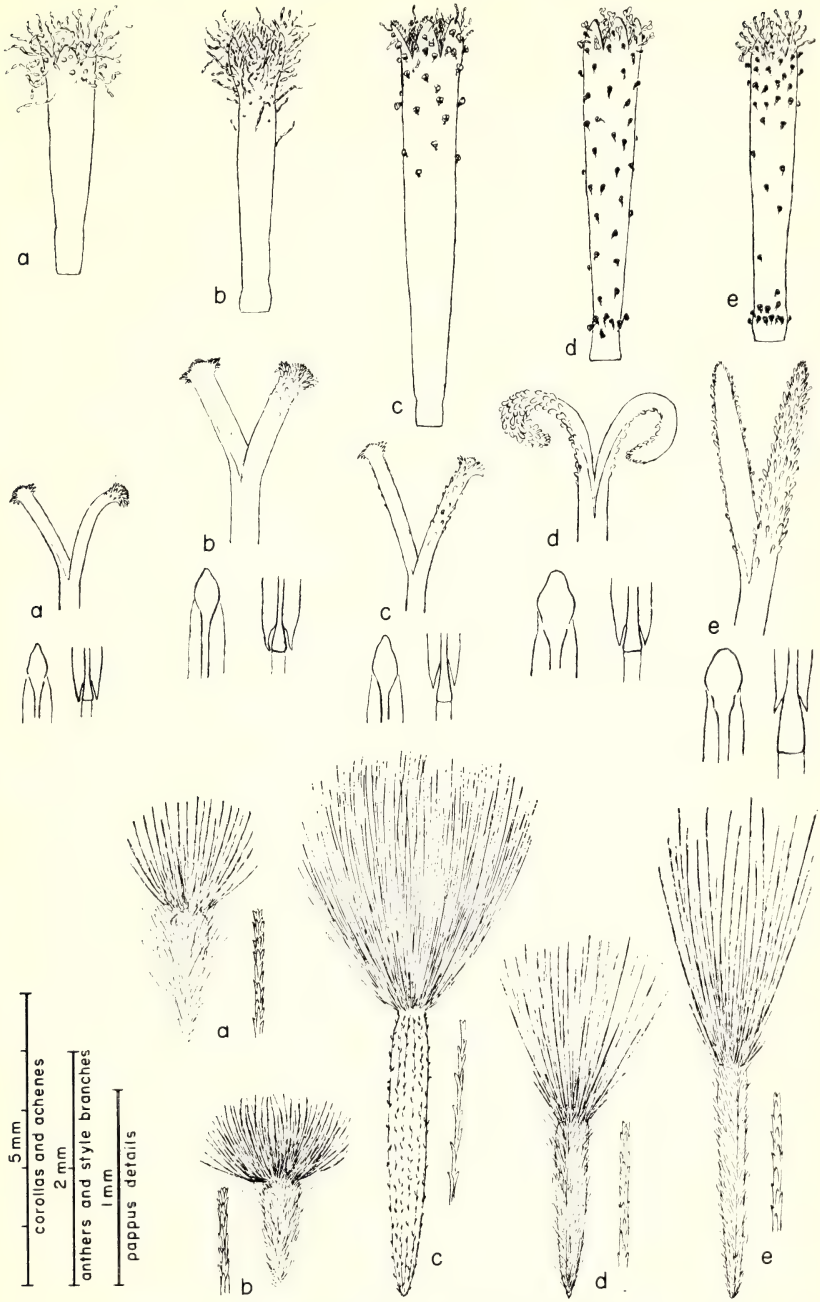

FIG. 1. Sketches of corollas, style branches, anther apices and bases, and achenes of *Psathyrotes*. a. *P. annua* (*Pilz 1185*, UC); b. *P. ramosissima* (*Strother 1220a*, UC); c. *P. pilifera* (*Strother 1202d*, UC); d. *P. scaposa* (*Correll and Flyr 38324*, UC); e. *P. purpusii* (*Pilz 715*, UC).

1. PSATHYROTES ANNUA (Nutt.) A. Gray, Smithsonian Contr. Knowl. 5(6):100. 1853.—*Bulbostylis annua* Nutt., Proc. Acad. Nat. Sci. Philadelphia 4:22. 1848. Type: The actual locality cannot be determined with confidence (see McKelvey, 1955; Reveal and Spevak, 1967). "Rocky Mts., near Santa Fe." (protologue and label at GH), "Mts. of U. Calif." (label on holotype at K), no date, *Gambel s. n.*

Freely branched, compact annuals (rarely perennials) 6–12 (4–15) cm high, 8–20 (6–40) cm across when flowering. Stems often purplish, furfuraceous and, sometimes, loosely and weakly tomentose. Leaves greenish to gray-green, furfuraceous and with scattered, subsessile to stipitate, swollen glandular hairs (rarely weakly tomentose as well); petioles stoutish, 4–12 (3–35) mm long; blades 8–15 (4–18) mm long, 9–20 (6–24) mm wide (notably smaller distally), rounded-deltoid to subreniform, usually cuneate, distally weakly to saliently 5–7 (3–9) toothed (rarely a few leaves entire). Heads borne singly on axillary or supra-axillary peduncles 5–15 (1–28) mm long (consecutively shorter distally). Involucres narrowly turbinate. Outer phyllaries 5 (rarely 6), 4–5 (8) mm long, erect, herbaceous, furfuraceous and with minute, subsessile glandular hairs, weakly persistent or deciduous; inner phyllaries mostly 8 or 13, 5–7 (9) mm long, chartaceous basally, distally herbaceous and similar to the outer ones, deciduous. Receptacle foveolate; hispid. Florets 13–16 (10–21) per head. Corollas light yellow, sometimes turning reddish to purplish distally; tube ca 0.5 mm long; throat ca 3 mm long; lobes ca 0.8 mm long, erect, elongate-triangular, papillate within, externally villous and with bulbous-tipped, glandular hairs. Anthers ca 2 mm long; apices triangular-lanceolate; bases sagittate. Style branches rather slender, ca 0.8 mm long; rounded-truncate, papillate. Achenes ca 2.5 (2–3) mm long; narrowly obpyramidal; densely hirsute with tawny to rufous hairs 0.5–1.0 mm long. Pappus of 35–50 coarse, tawny to rufous, subequal bristles 2–3 (1–4) mm long in 1 series. Figure 1,a.

DISTRIBUTION (fig. 2): SW Idaho (Canon Co.), NW Nevada south to W Mojave Desert (Red Rock Canyon, Lucerne Valley, Twenty-nine Palms) east to W Utah (Tooele, Juab, and Washington counties) and NW Arizona (Mohave Co.). Locally common, mostly on alkaline soils in washes and playas between 800 and 2000 m, exceptionally to 450 m, in association with Creosote Bush Scrub, Shadscale Scrub, or Alkali Sink vegetation. Mid May to mid October.

Plants of *P. annua* and *P. ramosissima* are rather similar in gross morphological aspect and members of each species have been misidentified as the other many times. These misidentifications have doubtless contributed to erroneous geographic statements and to inaccurate morphological descriptions in regional and local floras. Geographic distributions of these species interdigitate and overlap in a few places (fig. 2). We have not found the two actually growing together, however, prob-

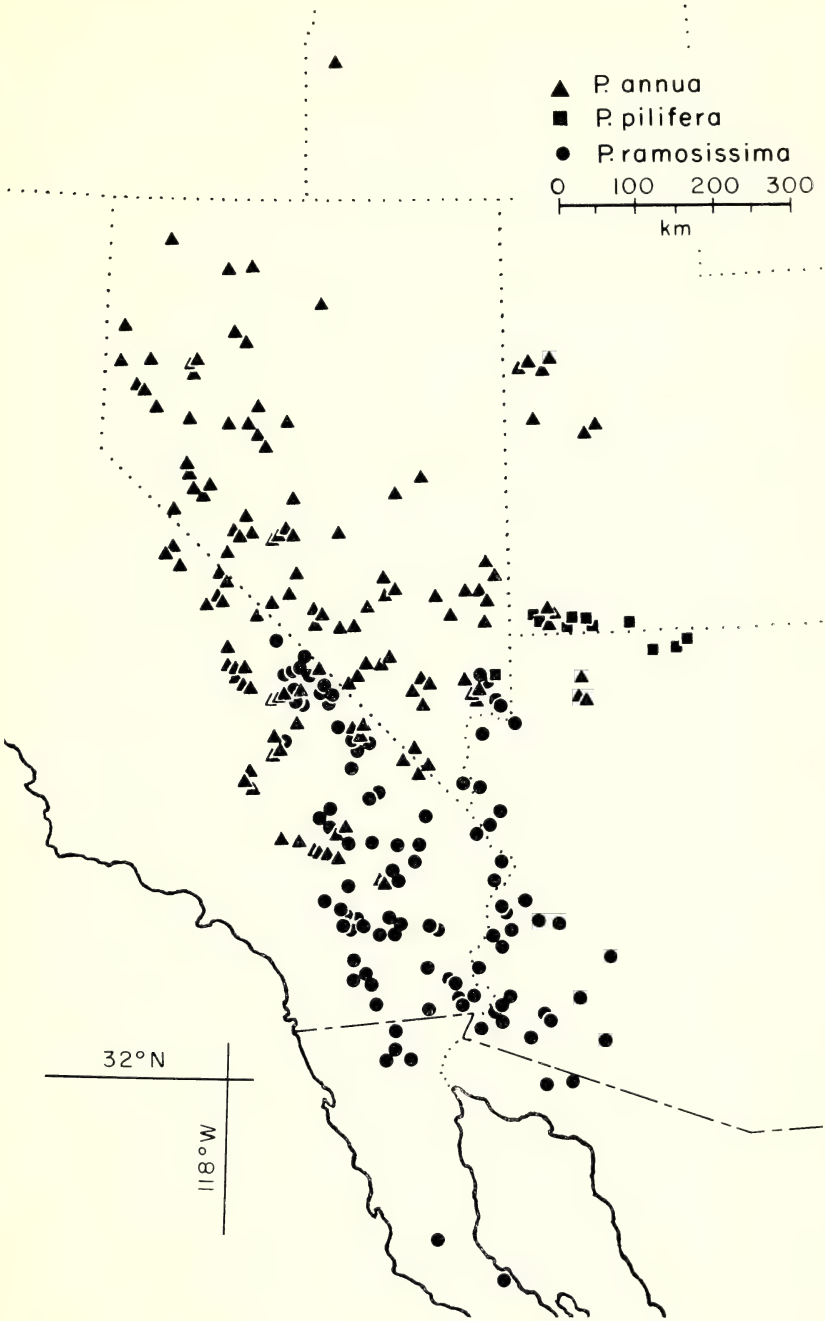

FIG. 2. Distributions of *Psathyrotes*.

ably because *P. annua* generally grows at higher elevations than *P. ramosissima*. But, in some areas of sympatry, plants of *P. annua* vary toward *P. ramosissima*, e.g., *P. A. Munz 14798* (CAS, GH, MO, POM), CA, Inyo Co., Panamint Mts. Wildrose Canyon, 2500 ft.; *Jack Reveal 47a* (UTC), CA, Inyo Co., Eureka Valley, sand dunes, 4800 ft.; *G. T. Robbins 3487* (JEPS), CA, Inyo Co., McLain Park, 8.8 mi S Shoshone, 1400 ft.; and *E. C. Twisselmann 4812* (CAS), CA, San Bernardino Co., Salt Wells Canyon, 1600 ft. These intermediates may be introgressants or they may be products of local selection pressures.

2. PSATHYROTES RAMOSISSIMA (Torr.) A. Gray, Proc. Amer. Acad. Arts 7:363. 1868. — *Tetradymia ramosissima* Torr., *In* Emory, Notes Mil. Rec. 145. 1848. Type: Arizona, southern Yuma Co., "Valley of Gila" (on holotype, NY!), "Hills bordering the Gila" (protologue), 18 Nov 1846, *Emory s. n.*

Freely and intricately branched, compact annuals or short-lived, often suffruticose, perennials 8–15 (3–30) cm high and 10–25 (5–40) cm across when flowering. Young stems lanate; older stems glabrate, shining. Leaves tawny to grayish green; lanate and furfuraceous, distinctly velvety; petioles stoutish, 7–20 (5–35) mm long, sometimes slightly purplish; blades 10–20 (8–25) mm long, 14–22 (8–30) mm wide (smaller distally), rounded-deltoid to subreniform or suborbicular, usually cuneate, distally 5–8 (3–10) toothed, the teeth low, rounded to obtuse-pointed. Heads borne singly on axillary or supra-axillary peduncles 5–15 (3–50) mm long (consecutively shorter distally). Involucres broadly turbinate to campanulate. Outer phyllaries 5 (rarely 6), 5–6 (4–10) mm long, spatulate or dilated at tip and spreading to squarrose or reflexed apically, herbaceous, furfuraceous and lanate and with minute, subsessile, glandular hairs, persistent, somewhat indurate, and strongly reflexed in fruit; inner phyllaries 12–15 (10–18), 6 (5–7) mm long, lanceolate, chartaceous basally, distally herbaceous and similar to the outer ones, deciduous. Receptacle foveolate; hispid. Florets 21–26 (16–32) per head. Corollas light or pale yellow, sometimes turning reddish or purplish distally; tube ca 0.5 mm long; throat ca 3.5 mm long; lobes ca 0.8 mm long, erect, triangular-lanceolate, papillate within, externally villous and with bulbous-tipped, glandular hairs. Anthers ca 2.5 mm long; apices triangular-lanceolate; bases sagittate. Style branches rather stout, ca 1 mm long; rounded-truncate, papillate. Achenes 2–3 (1.5–3.5) mm long; obpyramidal; densely hirsute with tawny to rufous hairs 1–2 mm long. Pappus of 120–140 tawny to rufous, subequal bristles 3–4 mm long in 2–4 series. Figure 1,b.

DISTRIBUTION (fig. 2): Death Valley region, Inyo Co., California, south through Mojave and Colorado deserts to vicinity of Bahia de San Luis Gonzaga, Baja California, east to Clark Co., Nevada, and the Colorado and Gila rivers in Arizona (Maricopa, Mohave, Pima, and Yuma

counties), and in NW Sonora. Locally common, mostly on sandy soils, often among dunes, sometimes on desert pavement, usually below 600 m, occasionally to 900 m, in association with Creosote Bush Scrub and desert dune vegetation. Mostly mid March to mid May, occasional throughout the year.

Errors on labels and morphological similarity between *P. annua* and *P. ramosissima* have contributed to inaccurate morphological and geographic circumscriptions for *P. ramosissima*. An apparent repeated source of error in reports of distribution of *P. ramosissima* is *Mrs. E. F. Shore 71* (NY), presumably collected near or at Reno, Nevada, in summer 1939. The nearest documented locality for *P. ramosissima* is more than 300 km southeast of Reno. Such a disjunction seems unlikely, and since the intervening area has been reasonably well collected, we believe that the locality given for *Shore 71* is an error.

Erroneous reports of *P. ramosissima* from Utah derive from two sources: misidentification of plants of *P. annua* [e.g., *M. E. Jones s. n.*, in 1896 (POM, US), Fish Springs; and *J. Langenheim 3824* (UC), Millard Co.] and an erroneous locality (St. George) associated with *E. Palmer 266,* in 1877 (NY, UC). Palmer was based in or at St. George in 1877 but he made several excursions including one to St. Thomas, Nevada, in April (McVaugh, 1956). His *"266"* was probably collected then.

3. Psathyrotes pilifera A. Gray, Proc. Amer. Acad. Arts 19:50. 1880. Type: Utah, Kane Co., "near Kanab", *Mrs. A. P. Thompson s. n.,* no date. Lectotype: GH! (Strother, Madroño 22:280. 1974).

Compact, freely branched annuals 6–15 cm high, 6–30 cm across when flowering. Stems tawny; glandular-pubescent and sparsely furfuraceous to subglabrous, sometimes with a few long, straight hairs. Leaves bluish green; sparsely furfuraceous, conspicuously ciliate on margins and veins below with straight, multicellular hairs 5–6 mm long; petioles 8–15 (5–18) mm long; blades 7–14 mm long, 6–14 mm wide (smaller distally), rhombic-rounded, cuneate, acute, entire. Heads borne singly from axils on peduncles 8–15 (4–20) mm long (consecutively shorter distally). Involucres narrowly cylindrical. Outer phyllaries 5, 6–9 mm long, narrowly lanceolate, erect, herbaceous, glandular-puberulent and usually with several conspicuous, straight, multicellular hairs ca 5 mm long, weakly persistent in fruit; inner phyllaries usually 8, 7–9 mm long, lanceolate-linear, mostly chartaceous but for the herbaceous tips, deciduous. Receptacle not pitted; glabrous. Florets 9–14 per head. Corollas pale yellow, sometimes tipped with reddish purple, very slender, cylindrical; tube ca 1 mm long; throat ca 6 mm long; lobes ca 0.8 mm long, erect, triangular, weakly glandular-pubescent with bulbous-tipped hairs and very sparsely villous externally. Anthers ca 3.5 mm long; apices triangular-lanceolate; bases sagittate. Style branches slender, ca 1.5 mm

long; rounded-truncate, papillate. Achenes 4–5 mm long; narrowly cylindrical to weakly fusiform; weakly ribbed; closely subscabrid to subglabrate. Pappus of ca 150 whitish, fine barbellulate bristles ca 5 mm long in 2–4 series and basally connate. Figure 1,c.

DISTRIBUTION (fig. 2): Restricted to the Dixie-Corridor area in SW Utah (Kane and Washington counties) and adjacent Arizona (Coconino Co.) and Nevada (Clark Co.). Locally common and conspicuous on heavy, often reddish, alkaline soils between 500 and 1400 m in association with ecotones of Creosote Bush Scrub, Pinyon-Juniper, Blackbrush, and Shadscale vegetations (see Cronquist et al., 1972). Sporadic, apparently depending on timing of rains, late June to early October.

We have seen one collection of *P. pilifera* misidentified as *P. annua: Ripley and Barneby 6370* (CAS, NY), NV, Clark Co., 1 mi W Glendale, 19 Jun 1944.

4. PSATHYROTES SCAPOSA A. Gray, Smithsonian Contr. Knowl. 5(6):100. 1853. — *Pseudobartlettia scaposa* (A. Gray) Rydb., N. Amer. Fl. 34: 358. 1927. Type: Labels and protologue indicate "Stony hills above El Paso", May 1851, *C. Wright "1416"*. The actual type locality is probably considerably southeast of El Paso, Texas, but it cannot be determined with certainty. Holotype: GH!; isotypes: GH!, MO!, NY!, PH!

Short-lived perennials (often flowering the first year and behaving as annuals) 8–30 (40) cm high when flowering. Caudices few-branched below; current aerial stems little to freely branched above. Leaves mostly basal; greenish to grayish; loosely floccose-tomentose; petioles 2–3 (1–5) cm long; blades 3–4 (1–6) cm long, 2–3 (1–4) cm wide, broadly lanceolate to ovate or rounded-deltoid, cuneate, margins crenate to subentire. Heads borne in tight to loose corymbiform clusters, terminating the branches of the glandular-puberulent, scapiform stems. Involucres broadly campanulate to hemispherical. Phyllaries 16–20 (8–21); obscurely in 2–3 similar series; 4–6 mm long; narrowly lanceolate; apically ciliate; dorsally glandular-puberulent; persistent and strongly reflexed in fruit. Receptacle not pitted; glabrous. Florets 25–40 (16–50) per head. Corollas bright yellow to almost white; tube ca 0.5 mm long, constricted; throat cylindrical, ca 4 mm long; lobes ca 0.5 mm long, erect to spreading, short-villous; throat and lobes bearing bulbous-tipped, glandular hairs. Anthers ca 3 mm long; apices ovate, blunt; bases weakly sagittate. Style branches ca 2.5 mm long; often curled; shaggy-papillate; rounded or conical at tip. Achenes 2.5–3.5 mm long; very narrowly obconical; sparsely hirsute with tawny hairs ca 0.5 mm long. Pappus of ca 80 tawny to rufous, unequal, coarse, smooth, blunt bristles 1–3 mm long in 2–3 series. Figure 1,d.

DISTRIBUTION (fig. 3): W Texas (Brewster, Hudspeth, Jeff Davis, and Presidio counties) and adjacent Chihuahua. Locally common on gypseous, calcareous clays or on limestone outcrops between 750 and

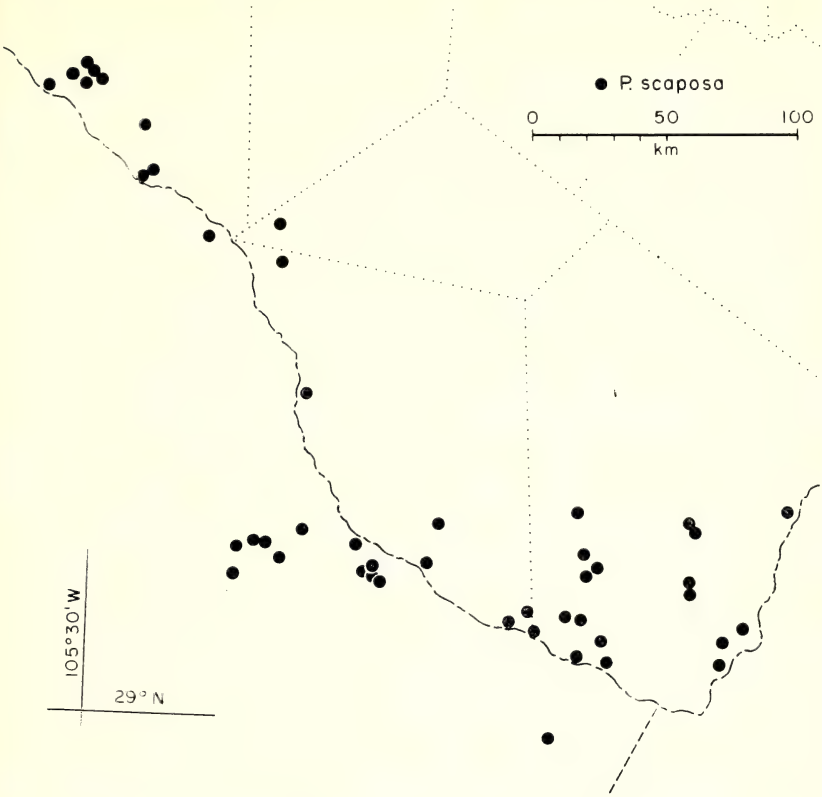

FIG. 3. Distribution of *Psathyrotes scaposa*.

1250 m in association with Creosote Bush Scrub vegetation. Bi-seasonal, late March to early May and in October, sporadic through summer.

Style branches have long been heavily weighted as a source of characters in classification of Compositae and the generally conservative nature of style branches indicates that such weighting is justified. The contrast then between the smooth, rounded-truncate style branches of the Sonoran Desert-Great Basin members of *Psathyrotes* and the shaggy-papillate, conically rounded style branches of *P. scaposa* and *P. purpusii* in the Chihuahuan Desert is unusual. This heterogeneity within *Psathyrotes* illustrates that expression of this character can vary even among closely related species and may serve as a caution against excessive reliance on style branch characters.

5. PSATHYROTES PURPUSII Brandeg., Univ. Calif. Publ. Bot. 4:193. 1911. — *Psathyrotopsis purpusii* (Brandeg.) Rydb., N. Amer. Fl. 34:360. 1927. Type: Coahuila, ca 100 km W Saltillo, "foot of Sombreritito, near Marte" (a railroad station), Oct 1910, *C. A. Purpus 7463*. Holotype: UC!; isotypes: GH!, MO!

Low perennial herbs from branched caudices. Stems of current season densely lanate. Leaves clustered at the tips of the branched caudex; loosely tomentose, gray-green above, densely lanate, canescent below; petioles 8–20 mm long; blades 12–28 mm long, 10–20 (30) mm wide, ovate to rounded-deltoid or subreniform, truncate to cuneate, margins distinctly and finely crenulate. Heads borne singly or in subumbellate clusters of 2–6 from upper axils on stout, woolly peduncles 8–20 mm long. Involucres narrowly to broadly turbinate. Phyllaries 15–21; obscurely in 2–3 series; 9–10 mm long; subequal; linear; woolly dorsally and ciliate apically; persistent and strongly reflexed in fruit; the innermost ones with narrow hyaline margins. Receptacle not pitted; glabrous. Florets 35–40 (20–50) per head. Corollas at first creamy yellow, becoming purplish apically; tube ca 0.5 mm long; throat ca 5 mm long; lobes ca 0.8 mm long, deltoid, erect to spreading, internally papillate, externally short-villous and with bulbous-tipped, glandular hairs. Anthers ca 3.5 mm long; apices ovate, blunt; bases weakly sagittate. Style branches ca 2 mm long; often curled; shaggy-papillate; rounded or conical at tip. Achenes 3.5–4.5 mm long; narrowly cylindrical; obscurely striate; sparsely hirsute with tawny hairs to 0.5 mm long. Pappus of ca 80 smooth, slender, unequal bristles 1–4 mm long in 2–3 series. Figure 1,e.

DISTRIBUTION: Known only from the type locality where we found it growing at ca 1200 m in light, sandy soil at the foot of talus (*Pilz 715*, 26 Jul 1971). July and October.

Excluded Names

Psathyrotes (Nutt.) A. Gray sect. *Peucephyllum* (A. Gray) A. Gray, Proc. Amer. Acad. Arts 9:206. 1874. ≡ PEUCEPHYLLUM A. Gray, Bot. Mex. Bound. 74. 1859. [Type: PEUCEPHYLLUM SCHOTTII A. Gray]

Psathyrotes incisa A. Gray, Mem. Amer. Acad. Arts, ser. 2. 5:322. 1854. [Type: California, "desert near the Rio Colorado" (protologue), "Desert west of Colorado" (label on holotype, GH!), Feb 1852, *Geo. Thurber s. n.*] ≡ TRICHOPTILIUM INCISUM (A. Gray) A. Gray, Bot. Mex. Bound. 97. 1859.

Psathyrotes schottii (A. Gray) A. Gray, Proc. Amer. Acad. Arts 9:206. 1874. ≡ PEUCEPHYLLUM SCHOTTII A. Gray, Bot. Mex. Bound. 74. 1859. [Type: Sonora, "Diluvial banks of the Colorado" (protologue), 3 Feb 1855, *A. C. V. Schott 45*. Holotype: GH! isotype: F!]

List of Exsiccata

Nearly 1000 herbarium specimens representing about 520 gatherings were examined during the course of this study (see list of herbaria in Acknowledgments). These, together with our field observations, are the basis of our descriptions, phenological statements, and distribution maps.

A list of *Psathyrotes* collections, arranged alphabetically by collectors' last names and chronologically by collection numbers or dates (for unnumbered collections) for each collector, is on file in UC and has been distributed to herbaria cited in Acknowledgments. Additional copies of the list are available from Strother.

Acknowledgments

We are grateful to curators and staffs of the following herbaria for loans of specimens and/or other courtesies: A, ASU, CAS, COLO, DS, F, GH, JEPS, MO, NY, OKL, OKLA, ORE, PH, POM, RM, RSA, SMU, TEX, UBC, UC, US, UTC, WIS, WS, and WTU. We are especially grateful to A. J. Hill, A. M. Powell, and S. Sikes for allowing us to include here their previously unpublished chromosome counts. This research was supported in part by NSF grants GB 7995 and GB 36647.

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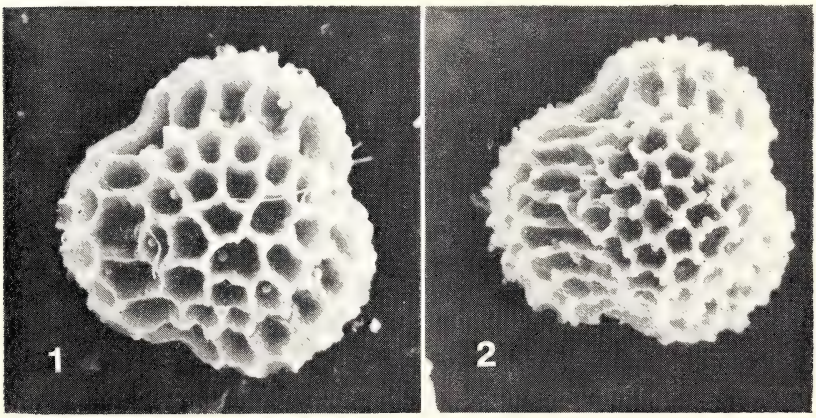
ANNOUNCEMENT OF MEETING.—The California Botanical Society will hold its second graduate student meeting 12–13 April 1975 at University of California, Davis. The meeting will take the form of a series of papers contributed by students. Members and non-members of the Society are invited to attend. For registration forms or other information contact LESLIE D. GOTTLIEB, Department of Genetics, University of California, Davis 95616.

SPHAEROCARPOS MICHELII BELL.: A NEW LIVERWORT FOR CALIFORNIA.—A population of *Sphaerocarpos michelii* was recently discovered growing on damp loamy soil along the bank of an ephemeral creek on the drier soil of a marshy portion of the creek bed where the creek crosses California Highway 91 about 18.2 km west of the junction of this road with California Highway 139 in Modoc County (*Doyle 1974*, UC). The plants were fairly abundant, but few sporophytes were present, and grew in association with three species of *Riccia*.

The female plants of *S. michelii* from Modoc County have small, terete bottles surrounding unfertilized archegonia and pyriform ones surrounding mature sporophytes and closely resemble female plants of *S. cristatus* Howe. *Sphaerocarpos michelii* grows intermingled with *S. texanus* Aust. in the United States (Bryologist 51:168–169. 1948). The female bottles of *S. texanus* are generally tubular to fusiform-clavate. Because of environmental plasticity of this character, however, details of spore markings and spore tetrad size are the best means to species identification. Spores of *S. cristatus* are separate at maturity, while those of *S. michelii* and *S. texanus* remain adherent as tetrads. In contrast to *S. texanus,* the spore tetrad of *S. michelii* is smaller, the walls of the reticulations are lower, and the intersections of the walls are elevated to form blunt spines (figs. 1–2).—WILLIAM T. DOYLE, Biology, University of California, Santa Cruz 95064.



FIGS. 1–2. Scanning electron micrographs of spore tetrads of *Sphaerocarpos* spp. 1. *S. texanus* (California: Monterey Co., *Doyle 1973,* UC), end view, ca × 361. 2. *S. michelii* (California: Modoc Co., *Doyle 1974,* UC) end view, ca × 472.

FLORAL BIOLOGY OF CALIFORNIA BUCKEYE

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California buckeye, *Aesculus californica* (Spach) Nutt., is a familiar tree or shrub of the Coast Ranges and Sierra Nevada foothills. It's phenology is unique among native deciduous trees, for although it is the first to leaf out in late winter, its leaves are the first to become senescent and die during midsummer. In contrast to this short active foliar period, the periods of floral and fruit development are quite long. Young inflorescences covered with hundreds of floral buds are exposed when leafing-out occurs; anthesis begins in spring and continues through early summer. Fruit development ensues from summer until winter when the large seeds are shed.

A closer look at California buckeye's reproductive method reveals anomalous features that apparently impede efficient sexual reproduction. For example, each spring trees are covered with candle-like inflorescences each bearing a profusion of odoriferous flowers that attract many insects; but apparently nectar and pollen are poisonous to honeybees, floral abscission is common, and relatively few capsules mature the following winter. The purpose of this study, therefore, was to examine the floral biology of California buckeye and in doing so to endeavor to resolve some of the presumptive paradoxes.

Study populations, each consisting of a stand of 40 or more buckeye plants within an area of about four hectares, were located throughout the species' range (fig. 1). Within each stand 20 individuals were tagged and used for analysis of floral form and occurrence, frequency, and distribution of bisexual flowers. Local populations in Alameda and Contra Costa counties (not shown in Figure 1) were used for experiments of floral development, pollination, and breeding behavior.

Floral Form and Development

Inflorescence primordia are laid down in fall within buds that also contain leaf primordia. When buds break in February and March, the inflorescences exposed are 5 to 10 mm long and tightly surmounted with small, undeveloped floral buds. The inflorescence elongates during spring by means of intercalary growth producing a columnar panicle (thyrse). Each lateral branch (cincinnus) bears from five to seven floral buds that mature one at a time. Within a given cincinnus, the bud nearest the rachis is the first to mature; its pedicel elongates, thrusting it out over the other buds. Subsequent bud development proceeds outward, although in most cases the outermost three buds never complete enlargement and fail to open. Bud mortality is even higher under adverse climatic condi-

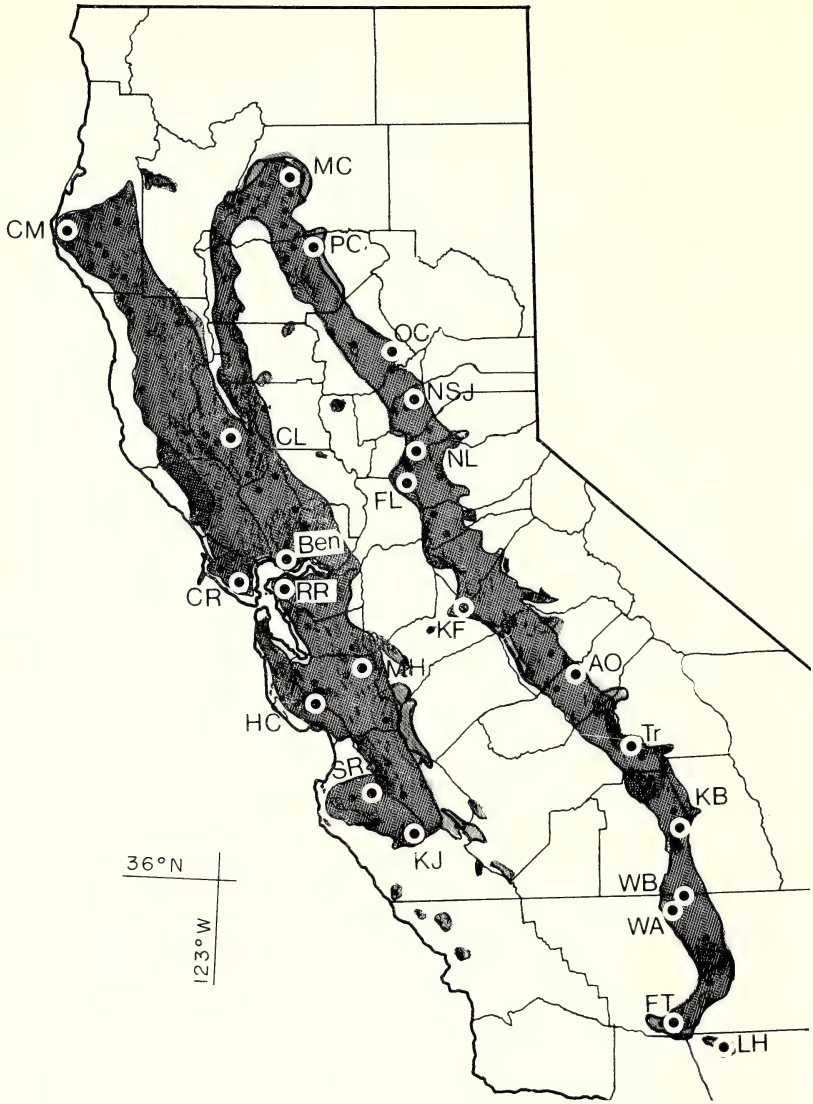

FIG. 1 Locations of study populations and the natural range of California buckeye.

tions, such as late frosts or early hot spells. Even with inherent bud mortality, an inflorescence may still bear over two hundred flowers.

Flowers of California buckeye are either bisexual or functionally staminate (fig. 2). In the former case, the gynoecium is fully developed and is composed of three fused carpels with two ovules per locule. In the staminate flower, the gynoecium is vestigial, with a stipitate, undevel-

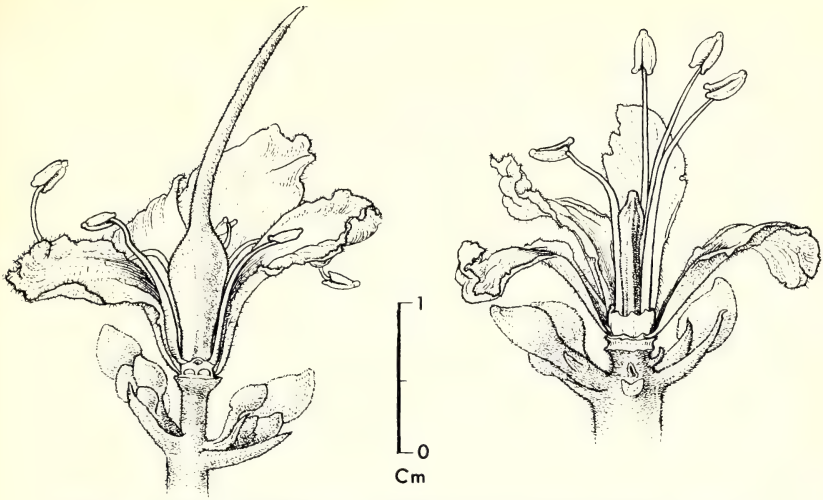

FIG. 2. Flowers of California buckeye. Left: bisexual; right: staminate.

oped ovary surmounted by a short, stubby style. Androecia of both kinds of flowers bear five to seven stamens, most of which are long-exserted at maturity.

After opening, a flower passes through a series of stages lasting 5 to 8 days. Bisexual flowers are protogynous. The flower commences anthesis with the emergence of the stigma and corolla through the enveloping calyx. The expanding white petals then reflex, exposing the villous pistil and orange anthers borne on short filaments. Yellow nectar guides then appear above the claws of the petals while the pistil with its long, pointed style completes its growth and the filaments begin to elongate. With maturation, nectar guides turn pink to red, filaments elongate, and anthers dehisce; short stamens may dehisce before the exserted stamens. Ovary enlargement continues after the perianth and stamens have fallen away. Many of the ovaries are abortive and fail to form fruits with viable seed.

Early development of the perianth and androecium in the staminate flower is similar to that of the bisexual flower. Filament elongation is rapid and stamens are longer than those of bisexual flowers. Staminate flowers fall from inflorescences more easily than bisexual flowers; nevertheless, premature abscission of young flowers of both types is common. Often they wither and drop off before the anthers have dehisced.

Occurrence, Frequency, and Distribution of Bisexual Flowers

Usually, the first flowers to open, the terminal flower and those that follow suit shortly afterwards, are staminate. There are trees, however, that produce inflorescences with terminal bisexual flowers or bisexual flowers early in the sequence of inflorescence development. Such behavior

is characteristic of inflorescences and trees that produce relatively high numbers of bisexual flowers throughout the flowering period. This early indication of high bisexual flower potential in some trees was observed at the Humboldt County population (CM).

In order to assess intra-panicle production of bisexual flowers, inflorescences from 12 study populations and miscellaneous collections from randomly selected trees were examined and the distribution and frequency of bisexual flowers within the inflorescences recorded. At each study area, a single inflorescence bearing bisexual flowers was picked at random from each tagged tree. Sampling was done only after trees were in full bloom. The effect of crown position and cardinal aspect was checked with no correlation or pattern of variation being readily apparent.

The majority of bisexual flowers were formed only in the upper portions of the inflorescences. Of 298 inflorescences examined, 55 percent had bisexual flowers restricted to the upper one-third of the inflorescence; in 23.5 percent, they were limited to the upper two-thirds while 21.5 percent had bisexual flowers distributed throughout the entire length of the inflorescence. None of the inflorescences examined had bisexual flowers restricted solely to basal cincinni. These data agree with Jepson's (1936) contention that bisexual flowers are generally formed near the terminal end of the inflorescence. Hardin (1956), on the other hand, stated that in *A. californica,* bisexual flowers were very often scattered throughout the inflorescence or occasionally occurred only near the top. In other species of *Aesculus,* bisexual flowers are restricted to the basal portion or more often occur in any part of the thyrse (Hardin, 1956).

Those populations that lacked inflorescences with bisexual flowers distributed throughout the entire length (MC, OC, KF) were notable in producing fewer inflorescences with bisexual flowers. Inflorescences with bisexual flowers distributed throughout the rachises occurred most frequently in the CM and KJ populations. Inflorescences from these stands also had the highest numbers of bisexual flowers (Table 1). Based on an average production of 200 flowers per inflorescence, the relative proportions of bisexual flowers approached, and in some cases exceeded, 25 percent. Three trees were noted to produce inflorescences in which up to 35 percent of the flowers were bisexual. In one tree at the KJ population, bisexual flowers failed to produce functional anthers, hence were pistillate. Failure of anther and pollen development was observed in occasional bisexual flowers from other individuals, but not to the extent achieved by this tree. Although the CM and KJ stands, respectively, occur near the northern and southern limits of the species' distribution in the Coast Range, they differ ecologically despite their similarities in floral behavior. The CM population, on Cape Mendocino, is on a windy, exposed, seaward slope, whereas the KJ population, near King City, is on a sheltered, sandy bench bordering oak woodland and dense chaparral.

TABLE 1. FREQUENCY OF BISEXUAL FLOWERS WITHIN INFLORESCENCES OF CALIFORNIA BUCKEYE. See Figure 1 for locations of study populations. N = 20.

Population sampled	Numbers of inflorescences per frequency class			
	0–4	5–10	11–20	more than 20
MC	5	10	5	0
OC	9	10	1	0
NSJ	4	8	8	0
KF	11	9	0	0
KB	5	11	4	0
WA	7	9	3	1
FT	3	14	2	1
CM	0	7	7	6
CR	2	12	4	2
RR	3	15	2	0
Ben	5	10	3	2
KJ	4	6	6	4
Totals	58	121	45	16
Misc. indv.	13	22	15	8
Totals	71	143	60	24

With the exception of these two populations (CM, KJ), the overall frequency tally evinced the general observation that the production of bisexual flowers within inflorescences is low (Table 1). Even though about one-fourth (28.2 percent) of the inflorescences bore more than ten bisexual flowers per inflorescence, the ratio of bisexual to staminate flowers generally did not exceed five percent.

Modification of sex expression. It is not unusual to find on a given tree several inflorescences that are broken or mutilated to varying degrees. Inflorescences are often attacked by insects; moreover, inflorescences on lower branches and on low, shrubby California buckeyes are especially subject to browsing by deer. Closer examination of these inflorescences often reveals a high proportion of bisexual flowers among those remaining. While still in the bud stage, these inflorescences are often chewed and/or nipped in half, and many of the flowers that would have been staminate turn out to be bisexual. Of 227 naturally mutilated inflorescences scored in the field, 84 percent had bisexual flowers compared with 47 percent for nearby unmutilated inflorescences.

In order to ascertain whether this behavior could be induced, inflorescences at various stages of bud development were cut transversely in half. Trees at local populations with lower branches near the ground were selected for treatment; 175 inflorescences were mutilated and 175 control inflorescences were tagged. Following anthesis, the mutilated and control inflorescences were scored for the occurrence, frequency, and distribution of bisexual flowers. There was no correlation between time of mutilation, i.e., stage of inflorescence development, and subsequent formation and number of bisexual flowers. Overall, 63 percent of the muti-

lated and 54 percent of the control inflorescences bore bisexual flowers. Within trees, the total and mean numbers of bisexual flowers formed in the control and mutilated inflorescences did not differ significantly. When, however, only the lower portions of the inflorescences were compared, the differences were highly significant. The mutilated inflorescences bore 1,113 bisexual flowers as compared with 301 formed in the basal half of the control inflorescences. Mutilations failed to increase the total number of bisexual flowers, but did stimulate gynoecial development in the lower cincinni, the region in which few bisexual flowers are normally formed.

Variation of sex expression. In *Aesculus,* each individual plant supposedly produces both staminate and bisexual flowers, i.e., is andromonoecious. The degree of consistency of this condition within and between populations is unknown. Do some plants produce only one floral type, giving rise to some degree of androdioecism, or do they all produce both types? What proportion of inflorescences in a given tree actually form both staminate and bisexual flowers and how does this vary within and between populations?

Presence or absence of bisexual flowers was scored for the tagged trees plus 257 additional individuals at the study areas. Also, 792 individual buckeyes distributed throughout the species' range were examined and tallied as to whether or not they bore bisexual flowers. The procedure was to scan the crown with binoculars and tally with a counter. All inflorescences were scored in trees with less than 500 inflorescences. In trees with more than 500, the sample was in excess of 500 inflorescences and not less than approximately 25 percent of the total number of inflorescences on the tree.

Populations examined varied little from the andromonoecious condition, for all individuals produced staminate and most produced at least some bisexual flowers. Individual trees, however, differ in the proportions of inflorescences that bear bisexual flowers. Only seven (0.28 percent) purely staminate trees were found, while there were only four (0.16 percent) in which every inflorescence appeared to contain bisexual flowers. It is not uncommon to find individuals in which fewer than 10 percent or more than 70 percent of the inflorescences had bisexual flowers (fig. 3). In those with high proportions of inflorescences with bisexual flowers, the ratio of bisexual to staminate flowers also was high.

The basis for this overall bimodality becomes apparent when individual populations are analyzed. Histograms for each study population plotted by 25-percentile classes are shown in Figure 4. Most of the trees in the coastal populations produced bisexual flowers in over 75 percent of their inflorescences. Moving inland, no consistent pattern was discernible. Trees in four populations (NSJ, NL, FL, TR) produced relatively high proportions of inflorescences bearing bisexual flowers, while the southern stands level off to a certain extent, having more or less

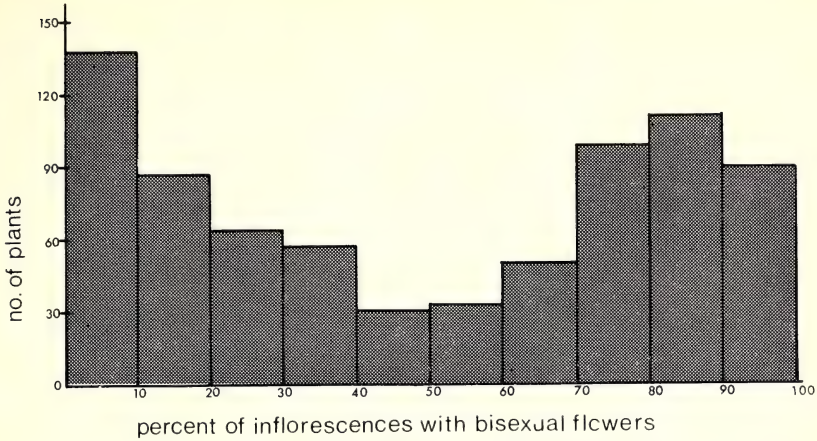

FIG. 3. Overall production of inflorescences with bisexual flowers in California buckeye.

equal numbers of trees in each class. Trees in the northeastern populations (MC, PC, OC), on the other hand, were notable in producing low proportions of inflorescences with bisexual flowers as were stands on the east side of the Mount Hamilton Range (MH) and in the Sierra Nevada foothills (KF). The low rainfall and extreme temperatures that characterize these inland habitats could be factors influencing sex expression. Climatic data from each site, however, would be necessary before attempting any specific correlations. Age of the plants might also be an important factor; in a sprouter like California buckeye, age of plant and age of aerial shoot are separate phenomena. The relative ages and form of the existing shoots that were included in the sample did not seem to influence production of bisexual flowers. Nevertheless, young sprouts were observed to form few, if any, inflorescences with bisexual flowers.

The relevancy of the above data depends on how they might vary with time. A 2-year survey in eight of the study populations showed an annual shift of 10 percent or less. Tally of 15 trees over an 8-year period indicated little year to year variation. Trees in extreme classes were most consistent.

POLLINATION AND BREEDING BEHAVIOR

Pollen grains of *Aesculus* are small and morphologically similar (Hardin, 1957); however, comparison with the published dimensions of other species indicate that the grains of *A. californica* are among the smallest, i.e., ca 19 $\times$ 25 μm. This is especially small for an entomophilous taxon. In addition, pollen production per anther is high, as is production on a flower, inflorescence, plant, or population basis.

Estimates of pollen production were based on counts of flowers and stamens from ten inflorescences randomly selected from collections from

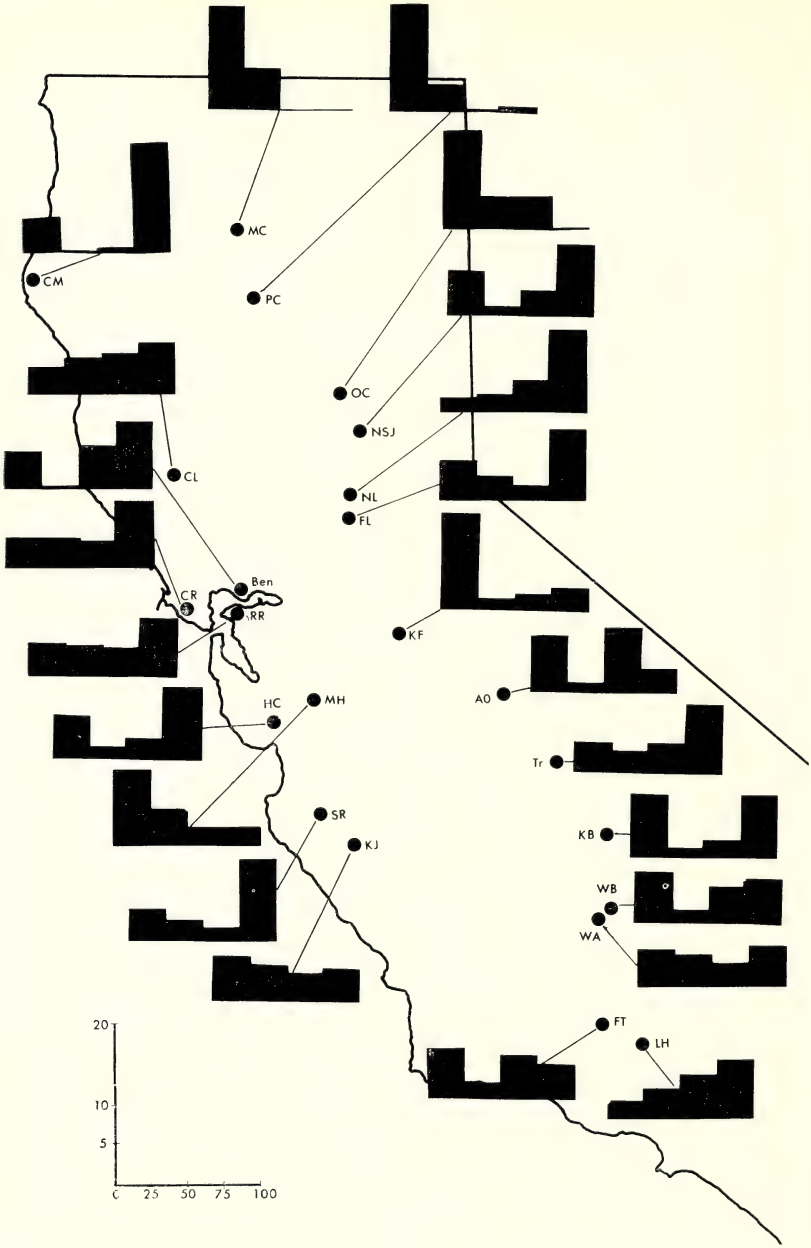

FIG. 4. Geographic variation in the production of inflorescences with bisexual flowers in California buckeye. Each histogram depicts relative proportions of inflorescences with bisexual flowers at each study population by 25-percentile classes. The vertical axis indicates numbers of plants.

the study populations. One anther per inflorescence was sampled. The number of pollen grains was estimated by emptying the contents of an undehisced anther into a drop of lactophenol-cotton blue on a slide. The pollen was evenly distributed with a needle and carefully covered with a coverslip. A 20 percent sample of the area under the coverslip was counted using a magnification of 100× and taking evenly distributed fields of view. The total number of grains estimated per anther ranged from 8 to 11 thousand. The stainability of the pollen generally exceeded 85 percent, so fertility presumably was quite high.

Pohl (1937) estimated that 42 million pollen grains are produced per inflorescence in *A. hippocastanum;* my estimate for *A. californica* is 19 million. He also gave a production figure of 451,543 pollen grains per ovule for *A. hippocastanum;* a conservative estimate for *A. californica* is 750,000. More meaningful as far as reproductive capacity is concerned is the number of pollen grains produced per seed. Most mature capsules in *A. californica* contain only one or two seeds even though the ovary of a bisexual flower forms six ovules (Hardin, 1955; Benseler, 1968). On a per seed basis, the above estimates would be increased three to six times. Even on a per ovule basis, pollen production by *A. californica* appears to be higher than other entomophilous and even some anemophilous woody plants (Pohl, 1937).

In order to test the possibility of some degree of wind pollination in California buckeye, pollen traps were placed in trees at local populations following the technique of Hoekstra (1965). Only nine buckeye pollen grains were found distributed among seven of the 140 pollen traps set out. The grains are sculptured and sticky and the stigma is hardly suitable for collecting airborne pollen. Externally, the stigma appears to be no more than the pointed end of the style. Microscopic examination of longisections through the tapered style revealed the stigmatic surface to be a chamber at the apex. This apical chamber divides into three canals, each of which courses through a carpel. With wind as the vector, success in this difficult pollen placement would be highly unlikely.

Insect Visitors. The abundance and variety of insects actively visiting California buckeye flowers were assessed at all the study areas. Representatives of over 40 genera and 19 families were collected, of which 56 percent of the species were Lepidoptera and 17 percent Hymenoptera (Table 2). The remaining 27 percent, distributed among Coleoptera, Diptera, Hemiptera, and Neuroptera, were innocuous insects incapable of pollination.

Honeybees *(Apis mellifera)* were active and abundant at all study areas. Honeybees have been reported as common pollen and nectar gatherers in *Aesculus* in Europe (Knuth, 1908; Kugler, 1336; Sussenguth, 1936). Close observation of their activities in *A. californica* inflorescences led to the conclusion that their effectiveness as pollinators is very poor. Because of their small size, they pass under and rarely come in

TABLE 2. INSECT VISITORS (HYMENOPTERA AND LEPIDOPTERA) COLLECTED FROM CALIFORNIA BUCKEYE. *** = collected at all study populations; ** = collected at ½ or more of the study populations; and * = collected at ¼ to ½ of the study populations.

HYMENOPTERA
Honeybee, *Apis mellifera* L.***
Bumblebees, *Bombus bifarius* Cress., *B. vosnesenskii* Rad.
Miningbees, *Andrena sp., Halictus sp.*
Wasps, *Sphecidae, Vespidae**

LEPIDOPTERA
Common Checkerspot, *Euphydryas chalcedona* (Dbldy.)**
California Sister, *Limenitis* (*Adelpha*) *bredowi californica* (Butler)
Callippe Fritillary, *Speyeria callippe* (Bdv.)
Mylitta Crescent, *Phyciodes mylitta* (Edw.)
Rustic Anglewing, *Polygonia faunus rusticus* (Edw.)
Mourning Cloak, *Nymphalis antiopa* (L.)
Buckeye, *Junonia coenia* (Hbn.)
California Ringlet, *Coenoympha california* West. & Hew.*
Satyrs, *Cercyonis pegala ariane* Bvd.
Hairstreaks: *Strymon adenostomatis* (Hy. Edw.), *S. saepium,* (Bdv.)*, *S. auretorum* (Bdv.), *S. californicum* (Edw.), *S. melinus* (Hy. Edw.)
Gorgon Copper, *Lycaena gorgon* (Bdv.)
Acmon Blue, *Plebejus acmon* (West. & Hew.)
Skippers, *Hesperia lindseyi* (Holl.), *Ochlodes agricola* (Bdv.)
Common Sulphur, *Colias eurytheme* Bdv.
Swallowtails, *Battus philenor* (L.), *Papilio eurymedon* Lucas, *P. rutulus* Lucas
Moths, *Agrotis ypsilon* Rott., *Peridroma margaritosa* (Haw.), *Eupithecia* sp.

contact with the anthers or stigmas as they crawl over the flowers collecting nectar. Even when foraging for pollen, they do not come near the stylar tip. Furthermore, pollen and/or nectar are toxic to worker bees as well as to larvae in the hives (Vansell and Todd, 1932; Eckert, 1933). Honeybees were frequently observed wandering aimlessly, as if in a stupor, over the inflorescences and eventually falling off and dying. It is important to note that the honeybee was first introduced into California in 1852 (Watkins, 1966); native insects do not seem adversely affected by the pollen or nectar. Thus we may rationalize the apparent contradiction of a plant poisoning an active pollinator.

Next to honeybees, the most frequent visitors were butterflies, the most common being the checker spot, *Euphydryas chalcedona.* Butterflies and a few moths observed at night appeared to be effective pollinators. They gathered nectar by traversing the length of the inflorescence, and in doing so, their flapping wings brushed against the anthers and the styles and thus could effect transfer of pollen grains into the stigmatic canal. *Aesculus parviflora,* which also has long stamens and styles, is pollinated by moths and butterflies (Knuth, 1908; de Wet, 1967) and perhaps even birds (Jaeger, 1961).

Despite the high pollen grain to seed ratio and the possibility of adequate pollen transfer by Lepidoptera, pollination still may be ineffectual.

Sampling of individual trees revealed that only about 10 percent of the gynoecia of bisexual flowers formed mature capsules. In many trees, gynoecial abortion exceeded 90 percent. Those trees that formed only a few bisexual flowers generally failed to form any fruit at all.

Compatibility. Patterns of insect activity observed suggested that most pollinations in California buckeye involve the transfer of pollen from flower to flower within a given tree (geitonogamy). Are these pollinations successful, resulting in fertilization and potential seed formation, or is outcrossing necessary? Moreover, is there any evidence of apomixis?

On nine trees at the local study areas, 352 flowers were individually tagged and were self- and cross-pollinated by hand or not pollinated. All of the latter (72) and 145 (73 self-pollinated and 72 cross-pollinated) of the others were isolated with Kraft paper bags. Of the 135 unbagged flowers, 68 were self-pollinated and 67 were cross-pollinated. The flowers tested were emasculated and all other flowers and buds in the inflorsecences were removed. Fresh pollen for cross-pollinations was collected at least 1 km from the study trees and was carefully applied with a brush to the stigmatic surfaces. The paper bags, 30 cm long, were placed over the entire rachis and taped securely around the peduncle. The bags were left in place for two weeks following pollinations. Ovary enlargement and fruit development were checked weekly.

No unpollinated flowers set seed, so apomixis is unlikely. Often, gynoecia dried up and the flowers dropped off before or soon after the bags were removed. Of the bagged, pollinated flowers, only seven formed single-seeded capsules; four of these were self-pollinated and three cross-pollinated. The unbagged, pollinated flowers formed only nine single-seeded capsules, of which six were from selfing and three from crossing. The few successful hand pollinations were not restricted to any one tree or locality; moreover the low numbers of isolated flowers to mature fruits cannot be attributed to unfavorable conditions in the paper bags. Self- and cross-pollinations were equally effective or ineffective. The trees used in the compatibility experiments produced average fruit crops, i.e., 5 to 10 percent of the bisexual flowers set seed; therefore, attempts to exceed natural seed set by means of hand pollinations were unsuccessful.

Conclusions

Aesculus californica is andromonoecious and despite high bud and floral mortality of both floral types, the ratio of staminate to bisexual flowers is extremely high. Heithaus et al. (1974) have suggested that such a condition may be a specialization for pollination by pollen vectors that have a large surface area as compared to stigma size. Production of large amounts of pollen, therefore, may be associated with buckeye's dependence upon large pollen vectors such as lepidopterids for successful deposition of small pollen grains into a small stigmatic chamber. Nevertheless,

although lepidopterids appear to be effective pollinators, seed set is low and there is no increase in seed set when stigmas are self- and cross-pollinated by hand. This low seed set suggests the disruption of gametophyte development, fertilization, or early embryogeny. Several million pollen grains are produced for every mature seed, an extremely wasteful condition for an entomophilous species.

Parallels are to be seen between *Aesculus* and certain species of *Eucalyptus* that also have terminal inflorescences with many flowers, bisexual flowers with pointed styles, and relatively large fruits and seeds (Carr et al., 1971). Both taxa exhibit a definite trend towards polygamy with sterilization of bisexual flowers and increased production of staminate flowers. The adaptive and evolutionary significance of such modifications is not clear. It might be allied to the pollination system described above and also to the problem of allocating resources and supporting the growth and development of large propagules. If every flower were bisexual and matured fruit, the plant might well self-destruct under the burden.

California buckeye can tolerate such anomolous floral conditions, breeding system, and low seed output because it is long-lived and a vigorous sprouter. The "survival of the fittest" does not necessarily imply that only the perfect persist, but rather survival is granted to those equipped to make it by whatever means available. Buckeye's sexual strategy may be inefficient from an evolutionary standpoint; nevertheless, its reproductive methods suffice under existing environmental conditions.

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RELATIONSHIPS OF TRACYINA AND RIGIOPAPPUS (COMPOSITAE)

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The relationships between *Tracyina* Blake and *Rigiopappus* Gray have been discussed briefly by various authors (e.g., Blake, 1937; Raven and Kyhos, 1961) but not until recently have the morphological characters of these monotypic genera been discussed in any detail. Van Horn (1973) and Robinson and Brettell (1973) suggest that despite their traditional placement in different tribes, these two genera are similar to each other in a number of respects, also resemble *Chaetopappa* and *Pentachaeta* (both Astereae), and properly belong in Astereae. In this paper we present additional evidence, from chromosomal, biochemical, and hybridization studies, that indicates unequivocally that *Tracyina* and *Rigiopappus* are very closely related to each other.

Methods and Materials

In 1960 the first author collected achenes of *Tracyina rostrata* Blake from the type locality (Alder Point, Humboldt County, California, *Ornduff 6185,* UC), one of two sites at which this rare species is known to occur (Keck, 1959). Plants of this annual species have been grown at the University of California Botanical Garden on several occasions since the initial collection; these cultivated plants were used in this study. *Rigiopappus leptocladus* Gray is widespread in the western United States, and three collections of this species were used in this study (Mount Hamilton, Santa Clara County, California, *Ornduff 6045;* Lake Berryessa, Lake County, California, *Ornduff 6108;* Scott Mountain, Trinity County, California, *Ornduff 6273,* all UC).

Tracyina has a chromosome number of $2n = 9_{II}$, as does *Rigiopappus* (Raven and Kyhos, 1961). Plants of both species and their artificial hybrids were examined for their flavonoid constituents, using living plants or dried material that was processed according to a method outlined in detail elsewhere (Bohm et al., 1974).

Intergeneric Hybridization

Because of their small size, it is very difficult to emasculate the hermaphroditic florets of either species, but it was possible to hybridize *Rigiopappus* and *Tracyina* by applying pollen of the latter to the pistillate marginal florets of the former. Two hybrid individuals were obtained from a cross between these genera *(Ornduff 6273 × 6185)*. These plants were vigorous, attaining a stature greater than that of either parent, and were intermediate between the parents in foliar and pappus characters. Examination of 100 pollen grains stained with aniline blue-lactophenol indicated viabilities of 99 percent for the parents and 31 and 36 percent, respectively, for the two hybrids. Study of hybrid meiosis by D. W. Kyhos indicated at diakinesis seven bivalents plus a ring of four chromosomes. This configuration suggests a very high degree of chromosomal homology between these two taxa. Despite their moderate degree of pollen viability the hybrids produced no mature achenes.

Flavonoid Studies

Kaempferol, quercetin, and isorhamnetin were identified in *Rigiopappus,* each occurring in the form of 3-0-glucoside and 3-0-rutinoside. The kaempferol and quercetin glycosides are shared with *Tracyina,* but this genus lacks isorhamnetin glycosides. The intergeneric hybrids produced the flavonoids of the parents.

The simplest of the possible biosynthetic relationships among the three flavonoid constituents of these genera is a simple and linear one. Kaempferol, a compound shared by both genera, may produce quercetin by addition of a hydroxyl group. Isorhamnetin may be produced by means of an O-methylation of quercetin. This last biochemical step is apparently carried out by *Rigiopappus* and the intergeneric hybrids, but it does not occur in *Tracyina.*

Discussion

Rigiopappus, Tracyina, and *Pentachaeta* all have a similar habit, termed the "herba impia" habit by Blake (1937; see also Van Horn, 1973). *Tracyina* and *Pentachaeta* are both members of Astereae, but the tribal affinities of *Rigiopappus* have been a matter of dispute. Chiefly because of its marginal receptacular bracts that are internal to the ray florets, *Rigiopappus* has traditionally been assigned to Helenieae (e.g. Hoffmann, 1889; Cronquist, 1955; Keck, 1959). More recently, Robinson and Brettell (1973) have stated that the stamens of *Rigiopappus* are "Asterean in all respects". Indeed, marginal receptacular bracts are

known to occur in some species of typical genera of Astereae such as *Haplopappus, Petradoria, Bigelowia, Chrysothamnus* (Loran Anderson, pers. comm.), and *Solidago* (Morton, 1968), and in *Tracyina* there are occasional receptacular bracts interior to the ray florets. One of the most striking differences between the two genera is in the nature of the pappus, consisting of 24–40 capillary bristles in *Tracyina* and 3–5 awnlike scales in *Rigiopappus*. The 10–15 pappus bristles of the intergeneric hybrid are intermediate in width.

Chromosomal and biochemical similarities between the genera argue for a close relationship. Intergeneric hybrids are vigorous, produce some viable pollen, and show a high degree of chromosomal homology. Both genera have four of six flavonoid compounds in common. The flavonoid produced by one genus but not the other may require only a simple O-methylation of a compound occurring in both species, a chemical transformation that could be controlled by a single gene (Harborne, 1967). This evidence from diverse sources leads us to the conclusion that *Tracyina* and *Rigiopappus* are very close relatives that should be placed side by side in Astereae. One could, indeed, use this evidence to argue for the congeneric status of these two taxa. However, the magnitude of the differences between them in some pappus, achene, and capitular characters is sufficiently great that we believe both taxa should be maintained as distinct monotypic genera.

Acknowledgments

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HETEROSTYLY, HOMOSTYLY, AND FECUNDITY IN AMSINCKIA SPECTABILIS (BORAGINACEAE)

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Amsinckia is a small genus of Boraginaceae consisting of 10–15 species found primarily in California but occurring naturally north to British Columbia, south to Baja California, east to Utah, and disjunctly in southern South America. Weedy members of the genus have been introduced to Europe, South Africa, central and eastern North America, Alaska and the Yukon, and Australia. Five of the species in the genus are, at least in part, heterostylous, with populations that consist of plants with "pin" flowers, with long styles and short stamens, and "thrum" flowers, with short styles and long stamens. Heterostylous taxa of *Amsinckia* are all endemic to California. They appear to be edaphic endemics, restricted to slopes of loose shaly fragments in the South Coast Ranges, except *A. spectabilis* F. & M., which is restricted to stabilized sand dunes and coastal bluffs. Three of the heterostylous taxa, *A. vernicosa* H. & A. var. *furcata* (Suksd.) Hoov. in Jeps., *A. grandiflora* Kleeb. ex Gray, and *A. douglasiana* A. DC., exhibit a pronounced pollen dimorphism, with thrum pollen larger than pin pollen, and also possess thrum flowers that are larger than pin flowers. *Amsinckia lunaris* Macbr. exhibits a peculiar type of heterostyly with a variety of stamen and style length combinations and anthers inserted at two levels in the corolla (Ray and Chisaki, 1957a). All heterostylous taxa in this genus are self-compatible (Ray and Chisaki, 1957a; Ganders, unpublished).

The remaining species of *Amsinckia,* including all the widespread, weedy taxa, are homostylous, with anthers and stigma positioned at the same level in the corolla. Morphological, ecogeographical, and cytogenetic evidence indicates the homostylous taxa have been derived from heterostylous taxa, which are primitive in this genus. Conspecific homostylous and heterostylous populations occur in *A. spectabilis* and have also been reported in *A. vernicosa* var. *furcata* and *A. lunaris* (Ray and Chisaki, 1957a, 1957b).

Homostyly in Amsinckia spectabilis

The distribution of distylous and homostylous plants in *A. spectabilis* populations is unusual. Populations may be exclusively distylous, exclusively homostylous or contain pins, thrums, and homostyles. Furthermore, in mixed populations of distylous and homostylous plants, there is considerable variation in the degree of heterostyly among different plants, that is, the distance separating anthers and stigmas in flowers may vary. There is virtually a complete gradient from pins to homostyles to thrums (fig. 1).

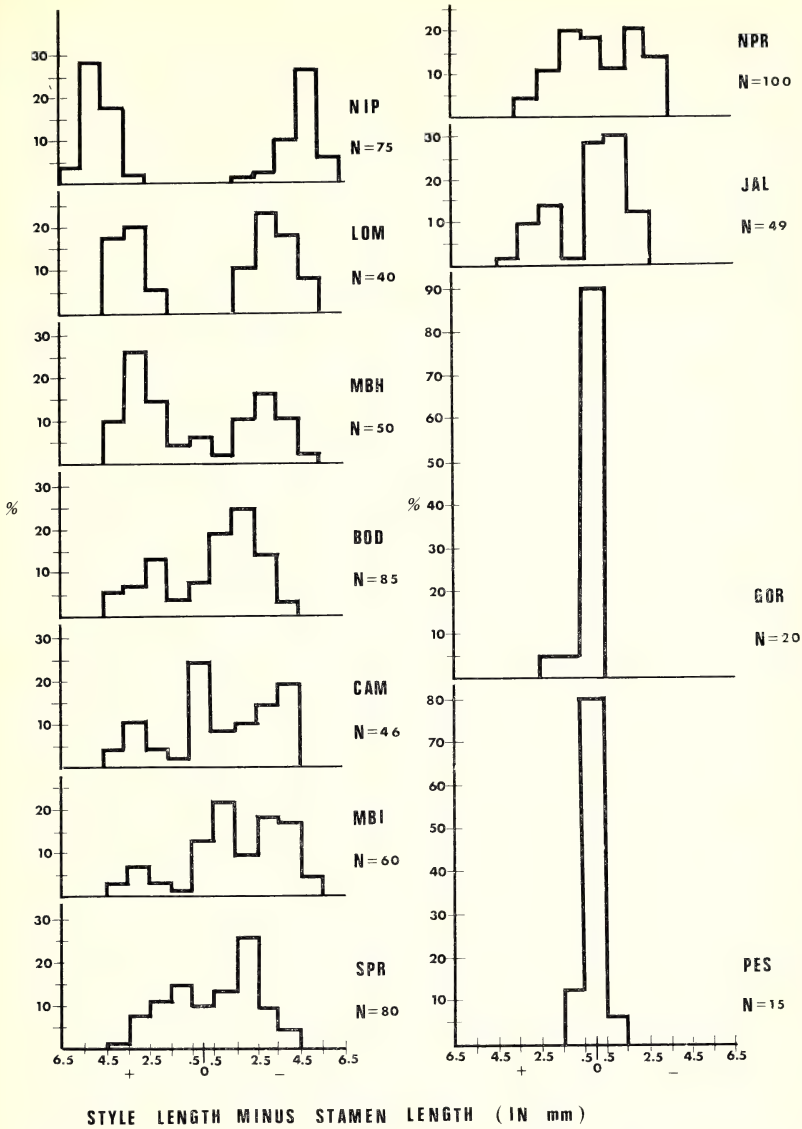

FIG. 1. Percentage frequency of stigma-anther separation classes in populations of *Amsinckia spectabilis* in California. Long styled flowers (pins) are to the left of 0 and short styled flowers (thrums) are to the right of 0. Locations of populations: (distylous populations) NIP—Nipomo, San Luis Obispo Co.; LOM—Lompoc, Santa Barbara Co.; (mixed populations) MBH—Henrietta Street, south side of Morro Bay, San Luis Obispo Co.; BOD—Bodega Bay, Sonoma Co.; CAM—Cambria, San Luis Obispo Co.; MBI—Inyo Street, south side of Morro Bay, San Luis Obispo Co.; SPR—South Point Reyes Beach, Marin Co.; NPR—North Point Reyes Beach, Marin Co.; JAL—Jalama Beach, Santa Barbara Co.; (homostylous populations) GOR—Goat Rock State Beach, Sonoma Co.; PES—Pescadero State Beach, San Mateo Co. N = sample size; one flower per plant was measured.

Unfortunately the genetics of this situation is not yet known. Ray and Chisaki (1957a) reported that a thrum × homostyle cross gave approximately a 1:1 ratio of thrums and homostyles in the progeny. Such a result is compatible with the interpretation that the homostyle allele represents a crossover of the *Primula* type, where thrum is dominant to pin. If this is so, it seems likely that other genes and possibly environmental factors are modifying the expression of the heterostyly alleles to produce the variation in degree of heterostyly found in these populations.

In mixed populations interbreeding between distylous and homostylous plants undoubtedly occurs; progeny from naturally pollinated homostyles contains pins and thrums. It is possible that these populations are evolving toward homostyly, but it is also possible that mixed populations have reached an equilibrium among the forms. Darwin (1877) grew seeds of *A. spectabilis* after Asa Gray suggested that several species in the genus were heterostylous, but because he found such a range of stamen and style lengths Darwin concluded that *A. spectabilis* was merely variable. Although prior to the work of Hoover (in Jepson, 1943) and Ray and Chisaki (1957a) the taxonomy of *Amsinckia* was hopelessly confused, there is no doubt that Darwin's plants were actually *A. spectabilis* var. *spectabilis,* since it is the only taxon in the genus that exhibits this type of variation. Darwin's record proves that such mixed populations have persisted for at least a century.

Homostylous and mixed populations and strictly distylous populations of *A. spectabilis* differ in several other morphological features and also in geographical range and are best considered infraspecifically distinct. Plants from the distylous populations [*A. spectabilis* var. *microcarpa* (Greene) Jeps. & Hoov.] have all five calyx lobes free to the base, have small mericarps (nutlets) 1.25–1.75 mm long, and the bifurcations of the cotyledons are flat and spreading. Distylous populations are restricted to Late Pleistocene sand dunes (the Orcutt Sand) in southern San Luis Obispo County and northern Santa Barbara County, California. *Amsinckia spectabilis* var. *spectabilis* consists of homostylous and mixed populations, two or three of the adaxial calyx lobes are fused one-half or more of their length, the nutlets are larger (1.75–2.33 mm long), and the bifurcations of the cotyledons are clavate and recurved. Flowers in this variety tend to be smaller and the plants tend to be more spreading in habit, branching from the base. *Amsinckia spectabilis* var. *spectabilis* is strictly coastal in distribution and ranges interruptedly from Guadalupe Island off Baja California to the Queen Charlotte Islands in British Columbia. The two varieties are interfertile and intergrade on the south side of Morro Bay, San Luis Obispo County, California. These populations, arbitrarily referred to var. *microcarpa,* may contain homostyles (fig. 1) and some plants with fused calyx lobes or a spreading habit. They retain the nutlet and cotyledon characteristics of var. *microcarpa.*

Mixed populations of *A. spectabilis* var. *spectabilis* occur only in Marin, Sonoma, San Luis Obispo, and Santa Barbara Counties. Strictly homostylous populations range north and south of the mixed populations

in Marin and Sonoma Counties, California (see fig. 1), and at least formerly they ranged south of the mixed populations in Santa Barbara County. Only homostyles occur outside of California. The homostylous populations in central California are small and the beaches where they occur have only small areas of suitable sandy habitats. On the other hand, the mixed populations are large and occur at Point Reyes and Bodega Bay where there are large areas of stabilized sand dunes. It might be noted that there are areas of apparently suitable sand dunes, such as at the mouth of Salmon Creek, Sonoma County, where the species has not been found.

Geographic distribution of mixed and homostylous populations strongly suggests that (1) homostylous populations were derived by colonization from mixed populations and (2) pins and thrums were selectively eliminated from the small founder populations. If monomorphic populations were derived solely by genetic drift in founder populations, monomorphic pin or thrum populations would also be expected, but they do not occur.

It seems reasonable to hypothesize that large mixed populations are sufficiently conspicuous to attract large numbers of pollinators, so that pins, thrums, and homostyles will all exhibit a high rate of seed set. In very small founding populations pollinator visits to flowers will be erratic and suboptimal for full seed set. If homostyles, because their anthers and stigmas are in close proximity, are capable of significantly higher rates of autogamous seed set than are pins and thrums, they will be at a great selective advantage. In small founding populations, homostyles will replace pins and thrums.

Materials and Methods

To test the validity of this hypothesis, autogamous seed set by the three forms was measured on plants grown in growth chambers. Pollinators were excluded, but the ventilation system of the growth chambers provided considerable air circulation, simulating the effect wind might have in nature in shaking pollen from anthers within flowers.

Seed set was measured on inflorescences collected from several large and medium sized natural populations where pollinators were presumably abundant. Inflorescences were collected from 13 pin and 21 thrum plants at Lompoc; 3 pins, 4 thrums, and 1 homostyle at Morro Bay; 13 pins, 5 thrums, and 28 homostyles at Jalama Beach; 3 pins, 8 thrums, and 7 homostyles at Cambria; 4 pins, 2 thrums, and 9 homostyles at North Point Reyes Beach; and 15 homostyles at Pescadero State Beach. For seed set measurements, homostyles were defined as plants with flowers in which the distance from the center of the anthers to the stigma was 1.5 mm or less. Only one very small mixed population was found during this study, at Atascadero State Beach on Morro Bay in San Luis Obispo County. The population consisted of nine plants in 1971, but seed set data were not obtained that year. In 1972, when seed set was measured, the population consisted of only two plants, one pin and one homostyle.

Results

In growth chambers, thrums set 196 out of 1680 possible seeds autogamously (11.7 %). Pin flowers set 458 out of 4524 possible seeds (10.1 %). The difference between autogamous seed set in pins and thrums is not significant ($\chi^2 = 3.09$, $P > .05$). Homostylous flowers set 293 out of 352 possible seeds autogamously (83.2 %). Thus, without pollinator visits, homostylous plants set eight times as many seeds as pins or thrums.

Natural seed set was high (80 % or higher) in all forms in large populations (Table 1). In the distylous population at Lompoc and the mixed populations at Jalama Beach and Morro Bay there was a significant difference in seed set among the forms. Only at Morro Bay, how-

Table 1. Seed Set by Different Flower Forms in Natural Populations of Amsinckia spectabilis.

	Pin	Thrum	Homostyle
Lompoc, Santa Barbara Co. (var. *microcarpa*)			
seed set	1430	2092	
seed failed	78	248	
total	1508	2340	
percent seed set	94.8	89.4	
$\chi^2 = 34.12$; $P < 0.001$			
Morro Bay, San Luis Obispo Co. (intermediate between var. *microcarpa* and var. *spectabilis*)			
seed set	382	572	226
seed failed	82	144	26
total	464	716	252
percent seed set	82.3	79.9	89.7
$\chi^2 = 12.33$; $P < 0.003$			
Jalama Beach, Santa Barbara Co. (var. *spectabilis*)			
seed set	752	238	1446
seed failed	44	6	46
total	796	244	1492
percent seed set	94.5	97.5	96.9
$\chi^2 = 9.82$; $P < 0.01$			
Cambria, San Luis Obispo Co. (var. *spectabilis*)			
seed set	221	841	503
seed failed	23	71	33
total	244	912	536
percent seed set	90.6	92.2	93.8
$\chi^2 = 2.22$; $P > 0.1$			
North Pt. Reyes Beach, Marin Co. (var. *spectabilis*)			
seed set	699	354	1270
seed failed	69	30	126
total	768	384	1396
percent seed set	91.0	92.2	91.0
$\chi^2 = 0.58$; $P > 0.7$			
Pescadero State Beach, San Mateo Co. (var. *spectabilis*)			
seed set			1226
seed failed			50
total			1276
percent seed set			96.1

ever, were homostyles at an advantage over the other two forms. This population was smaller than other mixed populations studied, occurring in a vacant lot at a housing development in Cuesta-by-the-Sea. It appears that in large natural populations pollinators are sufficiently abundant that all forms have a high rate of seed set.

In 1972, the Atascadero State Beach population consisted of one pin and one homostyle. Population size was probably limited by the small area of suitable habitat, by human disturbance, and by abnormally low rainfall in 1972. Nevertheless, the population simulates a small founder population. On inflorescences collected, the homostyle set 30 out of 32 possible seeds (93.8 %) whereas the pin plant set 76 out of 136 possible seeds (only 55.9 %). The difference is statistically significant ($z = 3.99$, $P < .002$).

Discussions and Conclusions

In large populations where pollinators would be expected to find it advantageous to exploit *A. spectabilis,* all three forms have very high seed set. Under such conditions homostyles do not have a significant advantage in fecundity over the other two forms. Homostyles, however, are capable of a much higher level of autogamous seed set. Under conditions where pollinator activity is erratic or suboptimal, such as may occur in small populations, homostyles will be at a strong selective advantage.

These conclusions suggest the following model to account for the establishment and geographical distribution of homostylous populations. The model is necessarily a simplification in that it ignores the variation in degree of homostyly.

Small founder populations derived from mixed populations, either in nearby habitats of limited carrying capacity (due to the small extent of open, stabilized, sandy areas), or in distant habitats where long distance dispersal results in few colonizers, will evolve quickly toward complete homostyly. If, however, a founder population in a habitat of large carrying capacity increases in size quickly enough, pins and thrums may not be eliminated before the selective advantage of homostyly disappears. Also, if the founder population is near enough to a mixed source population so that dispersal is more or less continuous, migration will slow the elimination of distylous plants giving the founder population more time to reach the population size at which the selective advantage of homostyly disappears. Geographic distribution of suitable habitats for *A. spectabilis* is linear and patchy. One would expect populations distant from mixed source populations, where the migration rate is very low (probably close to zero), to be homostylous. Populations established nearby mixed source populations, however, would be expected to remain mixed, if habitat size is large and particularly if migration is also relatively high. Nearby founder populations in small habitats, where population size cannot become large, would be expected to become homo-

stylous unless the migration rate were extremely high, which would be the case only if the habitats were adjacent. The model is consistent with the known distribution of population types.

This means that over short periods of a few generations, population size determines the selective value of homostyly. After populations have reached carrying capacity, habitat size, by setting the upper limit to population size, determines the selective value of homostyly.

Finally, selection for autogamy in founding populations seems to be a sufficient explanation for the distribution pattern of populations in this species. It is unnecessary to postulate that autogamy is advantageous because it preserves certain closely-adapted genotypes—the "fitness" hypothesis first advocated by Mather (1943). This concurs with recent studies of the evolution of autogamy in other annual genera (Lloyd, 1965; Arroyo, 1973). These studies also support the view that autogamy is selected primarily under conditions of unreliable or inefficient pollinator availability.

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NOTES AND NEWS

Ranunculus flagelliformis Discovered in the Galápagos Islands.—No member of the Ranunculaceae had been reported from the Galápagos Islands by the end of 1970. Then, in June 1971, Paul A. Colvinaux and Charles Racine from Ohio State University discovered plants of a semi-aquatic *Ranunculus* near the summit of Mount Crocker on Isla Santa Cruz. Upon return to Ohio, Colinvaux sent me a sheet of the material and a slide bearing a preparation of its pollen.

An appeal was made to Daniel Weber, who was searching for orchids in the Galápagos Islands at the time, requesting that he look for good specimens of the *Ranunculus* around the higher flanks of Mount Crocker. He replied that he had already collected buttercups in that area during the previous February and forwarded a duplicate sheet of his specimens.

Weber's plants bore several flowers and heads of mature fruits. One flower was soaked and carefully dissected, and mature achenes were examined. A note on Weber's specimen read "Petals 3" and a check of the flowers available and of a well pressed one on Colinvaux and Racine's specimen indicated 4 or 5 sepals and 2 or 3 petals. Study of the two collections and comparison of them with material from Mexico and Central and South America showed the plant to be *Ranunculus flagelliformis* Smith.

Many descriptions of this species are brief or inadequate for making a determination of an unfamiliar plant (see Martius, Flora Brasiliensis 13:156–157, *pl. 33, fig. II*, 1864) so the following description and drawings (fig. 1) are presented.

RANUNCULUS FLAGELLIFORMIS Smith in Rees, Cycl. 29: no. 13. 1819. Plants perennial in shallow water or on muddy margins of pools; primary leaves 10–15 in tufts above slender, white, sparingly branched roots to 10 cm long; petioles erect, 5–20 cm long, 1.5–4.0 mm in diameter, glabrous below, appressed-strigose with upwardly pointing, golden hairs on terminal 2–4 cm of larger leaves; blades deltoid-ovate to suborbicular, 2.0–5.5 cm broad, 2.0–4.5 cm long, basally truncate to shallowly cordate, appressed-strigose on upper surface near petiole, otherwise glabrous, subentire to coarsely but shallowly crenate, 5–9-veined; 1 to several slender stolons spreading 30–50 cm from primary tuft of leaves, at least some of lower nodes rooting and with 1 or 2 small leaves and a single flower at each node; internodes 5–12 cm long; pedicels erect or ascending, 1.5–3.5 cm long, sigmoid, appressed-strigose with golden hairs 0.2–0.5 mm long; sepals 4(5), broadly ovoid, rounded at both ends, shallowly to markedly cucullate, 2.0–2.2 mm wide, 2.8–3.2 mm long, almost membranous, pale yellow-green, glabrous; petals 2(3), about 1.0–1.3 mm wide, 2.8–3.0 mm long, pale yellow with tinge of green toward base, obovate, the claw about 0.4 mm wide, 0.5–0.6 mm long; gland small, covered by a minute transverse scale; stamens few (6–12 in flowers examined), in groups of 2 or 3, filaments 1.0–1.3 mm long, half as thick as broad, strongly incurved; anthers golden yellow, 0.8–1.0 mm long; pollen grains ca 32–38 μm long, 21–30 μm wide, dark brown, irregularly reticulate-ridged; fruiting heads 4–6 mm long, 3–5 mm wide, bearing 8–15(20) achenes; mature achenes asymmetrically ovate, slightly flattened laterally, 1.6–2.0 mm long, 0.8–1.0 mm front to back, 0.3–0.5 mm thick, nearly smooth, but with several low, rounded, minute umbos on each side, a blunt apiculation 0.1–0.2 mm long at apex, a narrow ridge along outer, curved margin and a narrower one along the adaxial, nearly straight margin.

Specimens examined: Behind Cerro Bandera, Pampa Zone, in a pond, 580 m, (localized) Isla Santa Cruz, *Weber 1114*, Feb 1971 (DS); aquatic, in small pools on saddle between Mt. Crocker and "chimney", Isla Santa Cruz, *Racine and Colinvaux 60*, 26 Jun 1971 (DS).

There were minor differences in size and density of pubescence on petioles and blades when the early and late season specimens were compared, but these seemed no more than those shown by many species collected several months apart.

Alan B. Franklin reported in June, 1973, that no buttercups could be found in that year. Weber's characterization of "localized" probably indicates the distribution pattern, but it is also probable that this plant grows only during years of high precipitation. While collecting in anticipation of preparing *The flora of the Galápagos Islands* (Wiggins and Porter, 1971), I explored the region around Mount Crocker in January-February, 1964, and again in 1967, but found no *Ranunculus*.

Colinvaux (personal communication) reported that studies of sediment cores taken from bottoms of pools on Isla Santa Cruz indicated that pollen from this *Ranunculus* had been deposited over a considerable period.

I thank Colinvaux for telling me of his discovery and for the specimens he gave me. Also, I thank Weber for his generous gift of a beautifully prepared sheet and Alan B. Franklin for searching the higher parts of Isla Santa Cruz in 1973.—IRA L. WIGGINS, Department of Biological Sciences, Stanford University, Stanford, California 94305.

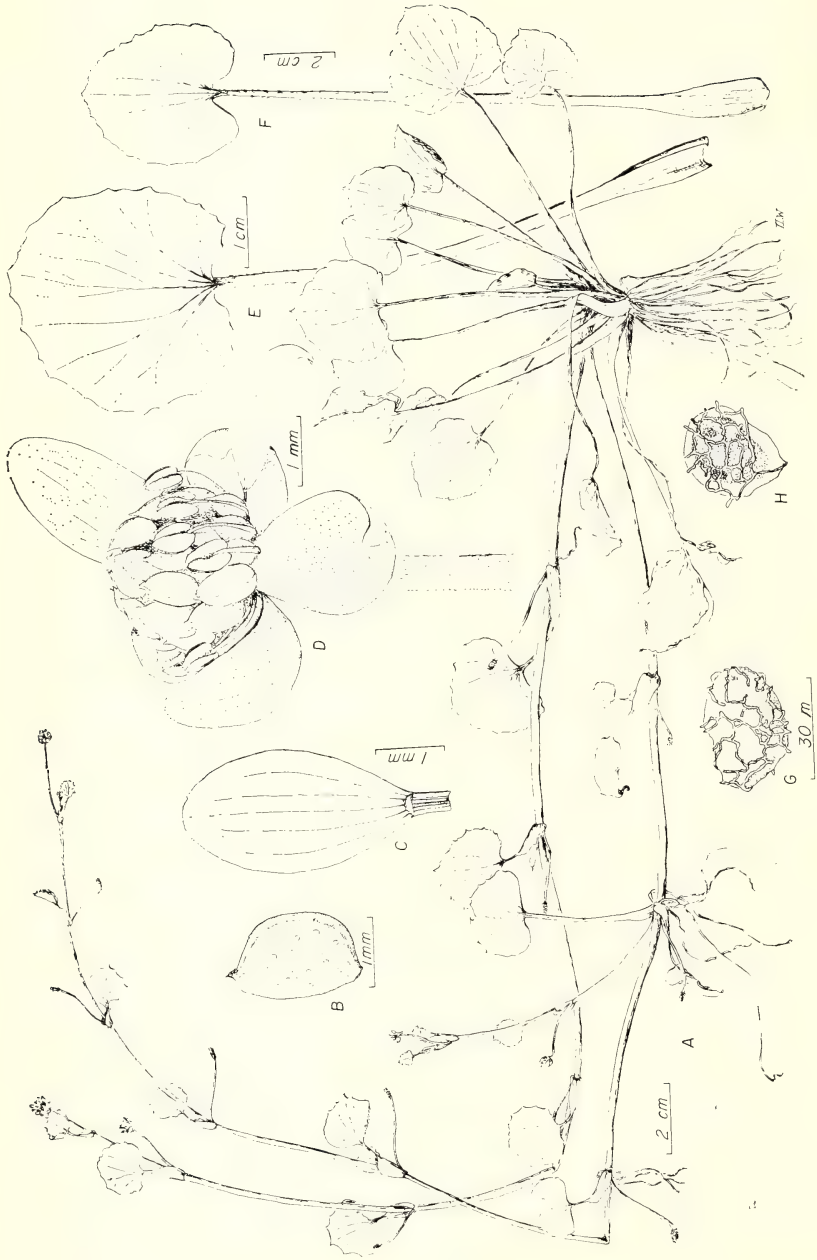

FIG. 1. *Ranunculus flagelliformis* Smith: A, Habit; B, Mature achene; C, Petal; D, Flower after dehiscence of anthers; E, Leaf (A–E from *Weber 1114*). F, Leaf; G and H, Pollen grains, from above and from side (F–H from *Racine and Colinvaux 60*).

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GEOGRAPHY OF POLLEN AND CHROMOSOMAL HETEROMORPHISM IN LEUCOCRINUM MONTANUM (LILIACEAE)

ROBERT ORNDUFF and MARION S. CAVE
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Sand-lily, *Leucocrinum montanum* Nutt., is a showy perennial that occurs widely in the arid regions of the western United States. Recently, the second author reported chromosome counts of $n = 11$, 13, and 14 for this species (Cave, 1970). Plants from the Rocky Mountain region have $n = 14$ (see also Löve et al., 1971), those from several localities in California, western Nevada, and Oregon have $n = 13$, and one population from Nevada has $n = 11$ (fig. 1). In addition, Cave noted that in some populations pollen is shed in tetrads and in others it is shed singly. In this paper we further discuss the variation in chromosome number and in the condition of pollen at the time of shedding.

In order to determine the condition of pollen at the time of shedding, all herbarium material of *Leucocrinum montanum* at the following institutions was examined: CAS, DS, JEPS, OSC, RENO, UC, and UO. Pollen was removed from the flowers, mounted in lactophenol, and subsequently examined microscopically. Pollen was also removed from the voucher specimens for the chromosome counts reported by Cave. Tetrad pollen for SEM investigation was obtained from flowers preserved in FAA. Monad pollen from herbarium material was rehydrated in water for 5 days, dehydrated in glacial acetic acid, acetolyzed for 3 minutes, and washed three times in water. Both types of pollen were placed in Swinny filter holders between two gold-coated Nucleopore filters, run through graded series to absolute ethanol, then to Freon TC, and critical-point dried. Tetrads were coated with chromium and monads with gold-palladium. Observations were made using a Coates and Welter model 50 SEM.

Pollen of *Leucocrinum montanum* is shed either in tetragonal tetrads or in monads (fig. 2). Although there are some morphological differences in wall sculpturing between the two populations we examined, we do not know if these differences are consistent throughout the species. With one exception, plants producing pollen in monads and those producing tetrads occupy allopatric ranges (fig. 1). Populations from the Rocky Mountain region, Utah, and central and eastern Nevada produce monads, the exception being a single collection from Lincoln County, Nevada, that produces tetrads (*Lehenbauer s.n.*, Joseco, RENO). However, another collection from the same area (*Wm. Mathews s.n.*, RENO) produces monads. Populations from extreme western Nevada and from California and Oregon all produce tetrads.

MADROÑO, Vol. 23, No. 2, pp. 65–104. April 1, 1975.

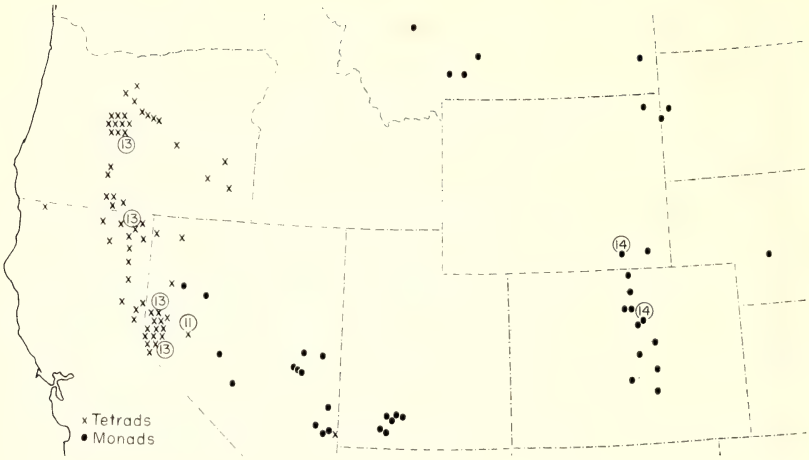

FIG. 1. Distribution of different pollen types in *Leucocrinum montanum* in the western United States. Numbers in circles indicate the chromosome number reported for populations in that locality.

The geographical variation in the nature of the pollen seems to be correlated with differences in chromosome number. Plants with $n = 14$ produce monads; those with $n = 11$ or $n = 13$ produce tetrads. There is one record of $n = 14$ for material from central Oregon (Assavesna, 1956) but preparations are not available for confirmation and this count must be accepted as provisional. In addition, Chambers (pers. comm.) reports that plants from Modoc County, California, have $2n =$ ca 50, with meiosis disturbed as a result of multivalent formation. It is likely that this population contains autotetraploid plants with $2n = 4x = 52$. Clearly the chromosome cytology of *Leucocrinum montanum* merits further study.

The occurrence of pollen tetrads is known in at least 50 angiosperm families (see Walker, 1971, pp. 10–11). Although we are not aware of the presence of pollen tetrads elsewhere in the Liliaceae (Nair and Sharma, 1965), tetrads are known in other monocot families such as the Amaryllidaceae and Velloziaceae. Monads and tetrads may be produced by different species in various genera, but the occurrence of intraspecific dimorphism in these traits is exceptionally rare. The only other example of which we are aware was reported by Walker (pers. comm.), who has discovered one specimen of *Eucommia ulmoides* Oliv. (Eucommiaceae) at the Arnold Arboretum that produces pollen in tetrads, while another specimen of the same species there produces monads. Whether this dimorphism occurs in the natural range of this Asian species is unknown.

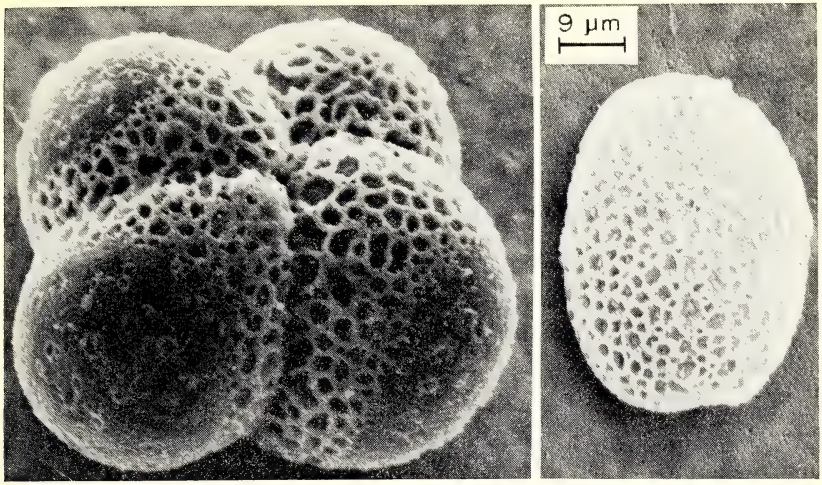

FIG. 2. Scanning electron micrographs of pollen of *Leucocrinum montanum*. Left: *M. Williams s.n.*, near Reno, Nevada, 1974 (UC). Right: *E. N. Brandegee s.n.*, Helena, Montana, 1898 (UC).

Although we have not made a detailed study of other morphological features of *Leucocrinum*, there are no evident consistent character differences associated with the pollen and chromosome variation noted above, and we believe that it is premature to suggest a taxonomic separation of these races. At present, we are also unable to explain the adaptive significance, if any, of the chromosomal and pollen heteromorphisms that are characteristic of this species.

We are indebted to Margaret Williams, Wayne Roderick, and C. L. Porter for providing us with living specimens of *Leucocrinum*, to J. W. Walker for information on *Eucommia*, to F. H. Smith and K. L. Chambers for assisting in other ways, and to Patricia Watters for technical assistance. Preparation of the pollen for the SEM work was supported by a grant from the National Science Foundation.

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THE GERMINATION LID: A CHARACTERISTIC OF THE LEMMA IN THE PANICEAE

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The presence of a hinged structure on the proximal surface of the lemma in *Setaria italica* (L.) Beauv. was first observed by Keys (1949). Rost (1975) further described this hinged structure in *S. lutescens* (Weigel) Hubb. and clearly demonstrated its role in germination. He also suggested its universal occurrence and possible taxonomic significance in the Panicoideae. The following study comprises an attempt to sample the Gramineae to determine the distribution and comparative structure of the germination lid.

Materials and Methods

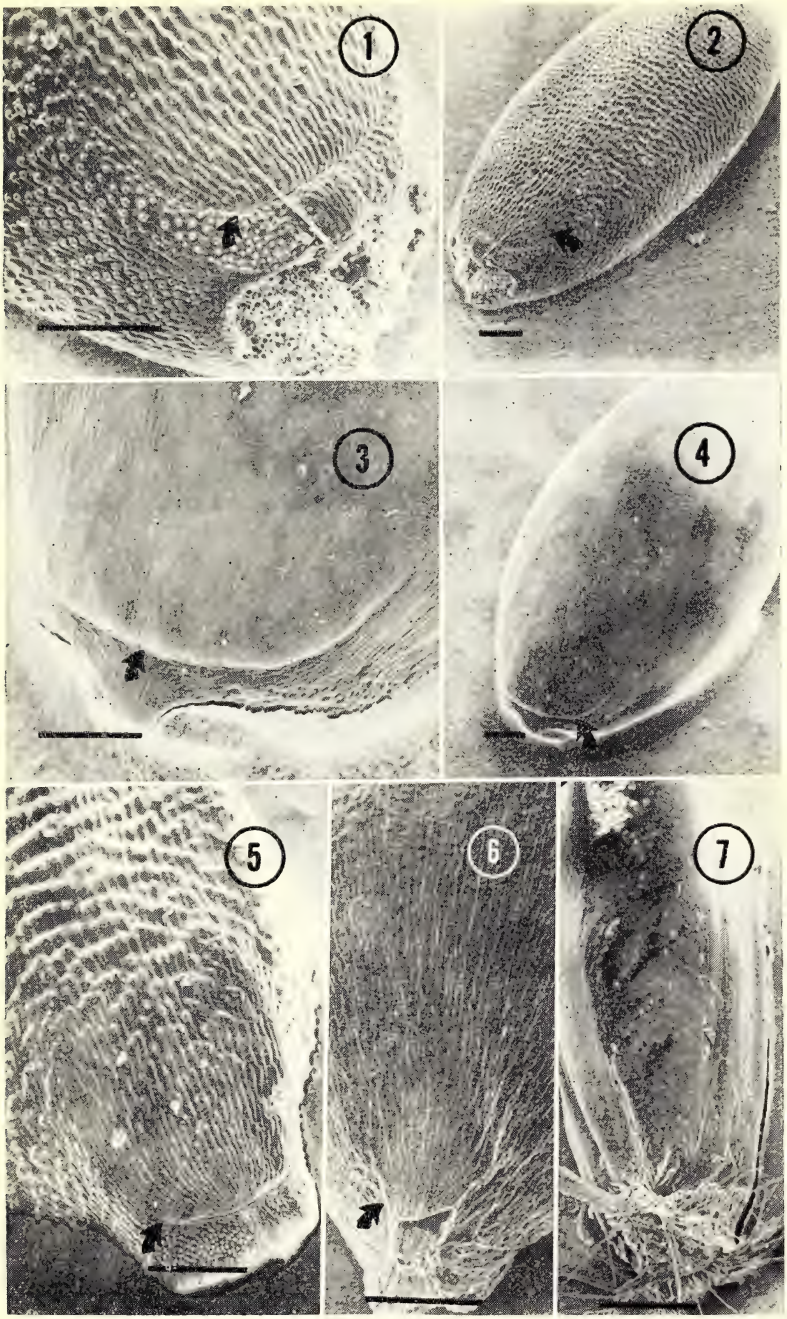
Florets were removed from herbarium sheets in AHUC and DAV. Other samples were supplied by Dr. Edward Terrell of the U.S.D.A. Plant Taxonomy Laboratory, Beltsville, Md. Crampton (1974), Hitchcock (1951) and Stebbins and Crampton (1961) were used as authorities on the Gramineae. Florets were soaked for 1 to 5 days in water to expand the embryos and make the germination lid, if present, more apparent. Measurements were made with an ocular micrometer mounted in an A/O stereo dissecting microscope. The scanning electron micrographs were taken of gold coated florets with a Cambridge Stereoscan S4.

Results and Discussion

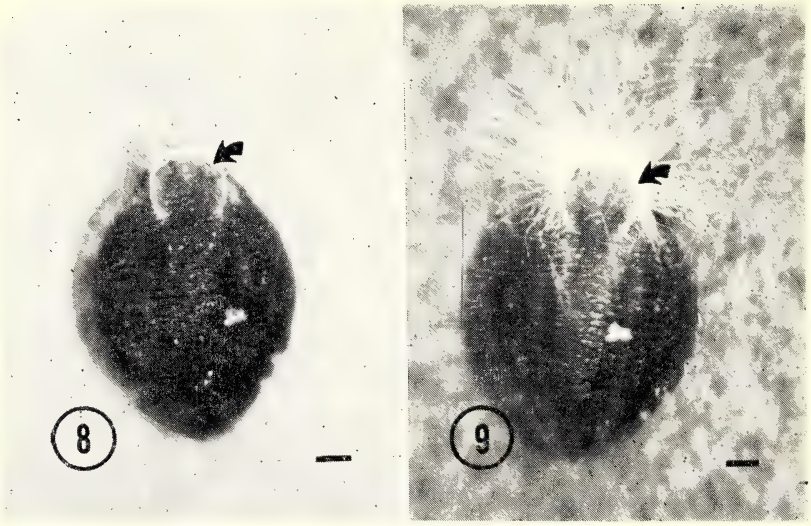
The taxonomic value of floret morphology has long been considered important in grasses. Reeder (1957; 1962) has shown the value of the grass embryo as a taxonomic character. For our study, 121 species were examined, representing 68 genera, 30 tribes, and 6 subfamilies.

The germination lid consists of a tiny hinged structure with a slightly indented outline located proximally on the surface of the lemma. The shape of the lid varies from a thin arc to a deep, almost square-shaped lid (figs. 1–6). During germination the coleorhiza forces open the lid, thereby facilitating easy passage through the usually hard, silicated lemma (figs. 8 and 9). The coleoptile emerges by forcing open the lemma and palea at the distal end of the floret, causing it to pivot open below and opposite the germination lid. Florets of Paniceae range from 10 mm to less than 1 mm in length. Germination lids range from 0.06–2.25 mm long $\times$ 0.17–0.75 mm wide. Most lids were approximately 0.25 mm square (Table 1).

Some contention exists as to whether certain genera (e.g., *Anthephora, Melinis,* and *Olyra*) belong in the Paniceae. Two members of *Anthephora* were examined: *A. pubescens* Ness. had a very papery lemma and showed



FIGS. 1–7. Scanning electron micrographs of grass florets. 1–6. Paniceae showing variation in germination lid shape. 1 and 2, *Eriochloa gracilis;* 3 and 4, *Panicum miliaceum;* 5, *Brachiaria ramosa;* 6, *Cenchrus palmeri.* 7, Floret surface morphology in *Andropogon ternarius* Michx. (Andropogoneae). All line scales equal 0.25 mm.



FIGS. 8 and 9. Germinating florets of *Setaria lutescens* showing opened germination lid with extended coleorhiza; line scales equal 0.25 mm.

TABLE 1. GERMINATION LID AND FLORET MEASUREMENTS FOR SELECTED MEMBERS OF PANICEAE. Size of lid varies with floret size and stage of development.

Species	Floret length (mm)	Lid length (mm)	Lid width (mm)
Amphicarphum purshii Kunth	2.60	0.37	0.50
Anthaenantia rufa (Ell.) Schult.	2.50	0.37	0.37
Anthephora hermaphrodita (L.) Kuntze	3.50	0.25	0.30
Axonopus affinis Chase	1.49	0.24	0.41
A. compressus (Swartz) Beauv.	1.82	0.24	0.33
Brachiaria ophyrodes Chase	2.62	0.37	0.50
B. praetervisa (Domin) Hubbard	2.50	0.50	0.50
B. ramosa (L.) Stapf	2.62	0.50	0.62
B. subquadripara (Trin.) Hitchc.	5.00	0.50	0.62
Cenchrus incertus M. A. Curtis	5.00	1.25	0.75
C. myosuroides H.B.K.	2.64	0.52	0.39
C. palmeri Vasey	6.25	2.25	0.75
C. pauciflorus Benth.	6.00	2.00	1.00
Digitaria ischaemum (Schreb.) Schreb. ex Muhl.	1.99	0.24	0.33
D. liniare Kratar	2.00	0.25	0.25
D. pentzii Stent	2.93	0.06	0.16
D. sanguinalis (L.) Scop.	2.75	0.37	0.37
Echinochloa colunum (L.) Link	1.08	0.26	0.49
E. crusgalli (L.) Beauv.	2.75	0.25	0.50
E. crus-pavonis (L.) Beauv.	2.76	0.23	0.66
E. frumentacea Link	3.00	0.50	0.62
E. haploclada Stapf	2.50	0.50	0.50
E. muricata (Michx.) Fernald	3.50	0.35	0.35

TABLE 1. *Continued*

Eriochloa contracta Hitchc.	2.51	0.43	0.43
E. gracilis (Fourn.) Hitchc.	2.64	0.39	0.59
E. lemmonii Vasey & Scribn.	2.50	0.25	0.50
E. montevidensis Griseb.	2.21	0.59	0.49
E. sericea (Scheele) Munro	2.75	0.62	0.62
Leptoloma cognatum (Schult.) Chase	2.25	0.19	0.16
Neurachne xerophila Domin	5.50	0.50	0.50
Olyra latifolia L.	5.50	1.00	1.00
Panicum agrostoides Spreng.	1.32	0.16	0.26
P. angustifolium Ell.	2.01	0.33	0.75
P. antidotale Retz.	1.68	0.26	0.56
P. capillare L.	2.50	0.50	0.62
P. condensum Nash	1.46	0.05	....
P. dichotomiflorum Michx.	2.07	0.22	0.50
P. hillmanii Chase	2.12	0.27	0.62
P. lassenianum Schmoll.	0.97	0.45	0.17
P. miliaceum L.	3.25	0.60	0.90
P. occidentale Scribn.	1.55	0.20	0.50
P. pacificum Hitchc. & Chase	1.40	0.25	0.92
P. scribnerianum Nash	3.37	0.50	0.87
P. thermale Boland.	1.61	0.26	0.41
Paspalum dilatatum Poir.	2.50	0.17	0.62
P. floridanum Michx.	4.25	0.50	1.50
P. notatum Flügge	2.87	0.25	0.75
P. quadrifarium Lam.	2.25	0.12	0.37
P. urvillei Steud.	2.37	0.16	0.79
Pennisetum typhoideum (L.) Rich.	3.75	0.50	0.50
P. villosum R. Br.	10.00	0.49	0.50
Setaria faberi Herrm.	2.08	0.49	0.50
S. geniculata (Lam.) Beauv.	1.90	0.50	0.50
S. lutescens (Weigel) Hubb.	3.25	0.50	0.50
S. macrostachya H.B.K.	2.20	0.37	0.50
S. magna Griseb.	1.83	0.33	0.49
S. reverchonii Pilger	2.89	0.37	0.50
S. scheelei (Steud.) Hitchc.	2.75	0.37	0.50
S. sphacelata (Schum.) Stapf & C. E. Hubb.	2.75	0.37	0.50
S. verticillata (L.) Beauv.	2.15	0.57	0.67
S. viridis (L.) Beauv.	2.38	0.25	0.25
Spinifex hirsutus Labill.	10.29	0.25	1.00
Stenotaphrum secundatum (Walt.) Kuntze	4.60	0.39	0.42
Trichachne californica (Benth.) Chase	2.33	0.16	0.33

no structure that could be clearly called a germination lid; *Anthephora hermaphrodita* (L.) Kuntze on the other hand had a clearly defined lid. On the basis of the presence of a germination lid in the latter species, we would retain *Anthephora* in the Paniceae, a placement advocated by Stebbins and Crampton (1961). *Melinis minutiflora* Beauv. does not have a germination lid and should, in our opinion, be once again segregated in the Melinideae of Hitchcock (1951).

Olyra has been variously placed. Hitchcock (1951) considered *Olyra* to be in the Paniceae, while Stebbins and Crampton (1961) placed it in

the Oryzoideae, tribe Olyreae. Reeder (1962) examined embryo characters and placed *Olyra* in the Bambusoideae. We examined *O. latifolia* L. and observed a large distinct germination lid almost 1 mm square and visible to the naked eye. This observation supports the placement of this genus in the Paniceae of Hitchcock (1951).

Twenty-five species of Andropogoneae from 16 genera and one species of Melinideae were examined (e.g., *Andropogon ternarius* Vasey, fig. 7); none of these Panicoid species has a germination lid. The five remaining subfamilies of the Gramineae were also examined; of 27 tribes and 30 genera none was observed to have a germination lid. The germination lid is, therefore, a feature found in the florets of the Paniceae. This character is suggested as an additional feature useful to determine generic relationships in the grasses.

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Two New Plants for Nevada.—*Camissonia cardiophylla* (Torr.) Raven subsp. *robusta* (Raven) Raven is now known from four stations in Clark County, Nevada: Black Hills, crevices in volcanic ridge near crest of mountain (Northwest Boulder City, SE¼ S16 T23S R63E), 1187 m, 12 Dec 1967, *V. Bostick 3225* (Univ. Nevada, Las Vegas); south end of Black Hills, steep rocky slopes (Northwest Boulder City, SE¼ S31 and SW¼ S32, T24S R62E), 1000 m, 11 Nov 1970, *V. Bostick 5253* (Univ. Nevada, Las Vegas); crevices in basalt cliff, southern exposure (Northwest Sloan, SE¼ S21 T24S R63E), 1187 m, 15 Feb 1971, *V. Bostick 5305* (MO). The range of this plant is hereby extended 129 km east from the Death Valley region, where this subspecies is found in washes at the base of the Panamint, Funeral, Grapevine, and Argus Mountains.

Asplenium resiliens Kunze is now known from one station in Nevada: southeastern Spring Mountain Range, south fork Pine Creek, north-facing cliff of Navajo sandstone, 1450 m, 16 Jun 1970, *J. C. Fisher, Jr., and G. R. Kennedy s.n.* (Univ. Nevada, Las Vegas). The range is here extended by 324 km to the west, the nearest location being the mountains about Flagstaff, Arizona. The entire range extends from southern Pennsylvania to Jamaica and Mexico, west through Illinois and Oklahoma to New Mexico and Arizona. It is notable that Pine Creek supports a relictual Pleistocene plant community in southern Nevada.—Jack C. Fisher, Jr., Biology Department, University of California, Riverside 92502.

TAXONOMIC STATUS OF VICIA HASSEI (LEGUMINOSAE)

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Eastern Kentucky University, Richmond 40475

The relationship between *Vicia hassei* and *Vicia exigua* has been a source of taxonomic confusion. Both taxa are annuals, setting seed by late spring or early summer. Both usually have one or two small inconspicuous flowers per raceme. *Vicia exigua* was described by Nuttall in Torrey and Gray in 1838. *Vicia exigua* of this paper refers only to California and Baja California populations attributed to that species. *Vicia hassei* was described by Watson in 1890, and Jepson in 1901 reduced it to a variety of *V. exigua*. More recent floristic workers (e.g., Howell, 1949; Munz, 1959; and Thomas, 1961) have followed Jepson's concept.

Materials and Methods

Specimens from the following herbaria were examined: ARIZ, BRY, CAS, COLO*, DS, F*, ISC, LA, MEXU*, MICH*, MIN, MO, NY, ORE, PH*, POM*, RSA, SBBG, SBM, SD, SMU, TEX, UARK, UC, US. Asterisks indicate selected material only was studied.

Buds collected from field and greenhouse plants were used for anther squashes, and root tips were used for karyotype studies (see Lassetter, 1972, for details). Voucher specimens are deposited at ISC. Field studies included procurement of mass collections as well as observation of pollinators and habitat characteristics. Plants were not fruiting during the field-work period, but viable seeds were obtained from herbarium specimens.

Results and Discussion

Examination of mass collections and herbarium specimens revealed two qualitative characteristics in *V. hassei* that are absent in *V. exigua*. Stylar pubescence in *V. hassei* is very dense and concentrated on the lower side of the style; this arrangement of hairs is termed the stylar brush. Secondly, the ovaries and legumes are pubescent (fig. 1). *Vicia exigua* has much sparser pubescence evenly distributed around the style (and, therefore, no stylar brush) and has glabrous ovaries and legumes (fig. 1). In addition, leaflet apices of *V. hassei* are mostly truncate or often emarginate with two or three mucros, whereas *V. exigua* leaflets are mostly acute or obtuse. These latter characteristics, however, are not wholly consistent, especially in young or stunted specimens of *V. hassei*.

Chromosome numbers in both taxa are $2n = 7$ II, and no meiotic irregularities were observed (Lassetter, 1972). All root-tip preparations counted were $2n = 14$. These numbers are the first reports for *V. exigua* Nutt. (sensu stricto) and *V. hassei*.

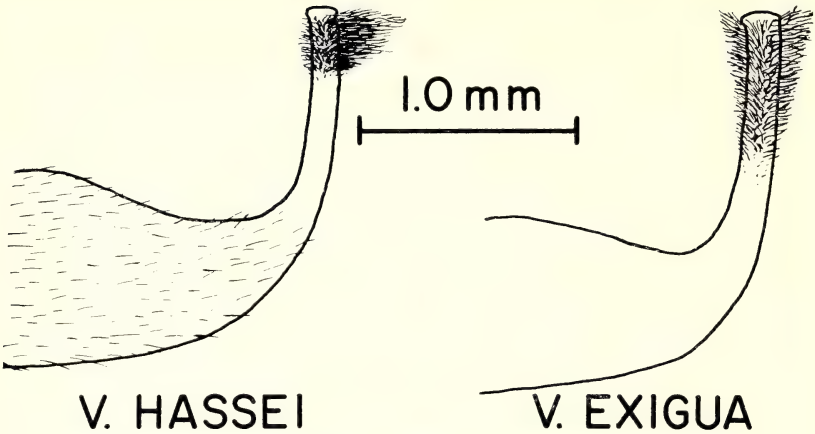

FIG. 1. Ovary apices, styles, and stigmas of *Vicia hassei* and *V. exigua*.

Karyotypes of *V. hassei* and *V. exigua* are given in Figure 2, and they obviously are different, as is most often the case in *Vicia* species (Sveshnikova, 1927; Shrivastava, 1963; Mettin and Hanelt, 1968). The largest two chromosome pairs in *V. hassei* are metacentric, with secondary constrictions very near the centromere. In *V. exigua,* no secondary constrictions were observed, and the smallest pair of chromosomes is satellited. Chromosomes of *V. hassei* are larger (fig. 2).

Field study revealed little difference in habitat preference between the two taxa, and both may be found in close proximity. Populations occur on a variety of soils, ranging from very sandy to rocky, but only *V. hassei* was found on fine-textured clay "dry-bog" soils.

Pollinators were not observed visiting flowers of these taxa. Bagging of greenhouse plants showed both taxa to be self-fertile, and bagging of single flowers indicated that the stigma receives pollen from anthers of the same flower. Because pollination usually occurs just before or sometimes at the time the flowers open, pollinators, even if present, probably would have little effect on intrapopulational cross pollination. Prolific fruit and viable seed were produced by several generations of each taxon under greenhouse conditions.

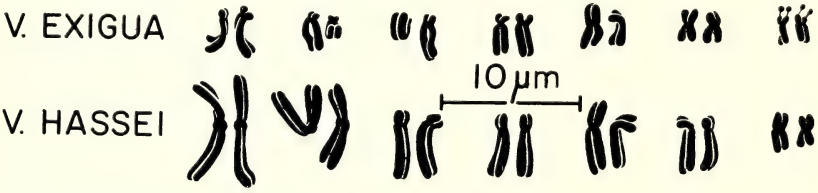

FIG. 2. Karyotypes of *V. exigua* (voucher grown from seed collected by *I. Marin s.n.,* ISC) and *V. hassei* (voucher grown from seed from DS 401987).

Distributions of these taxa, determined from my own collections and herbarium data, are given in Figure 3. *Vicia hassei* extends from Baja California to Southern Oregon and is not found farther east than the San Joaquin Valley. *Vicia exigua* is almost wholly restricted to areas south of Los Angeles except for one collection from Shasta County, California (*Eastwood s.n.*, in 1912, US!). *Vicia hassei* is strictly a west coast taxon, while *V. exigua* is the westernmost extension of a group of interrelated taxa of the *Vicia ludoviciana* complex (*V. ludoviciana* Nutt., *V. leavenworthii* T. & G., *V. exigua* Nutt., and their infraspecific taxa). Relationships of this Texas-centered complex will be presented in a later publication.

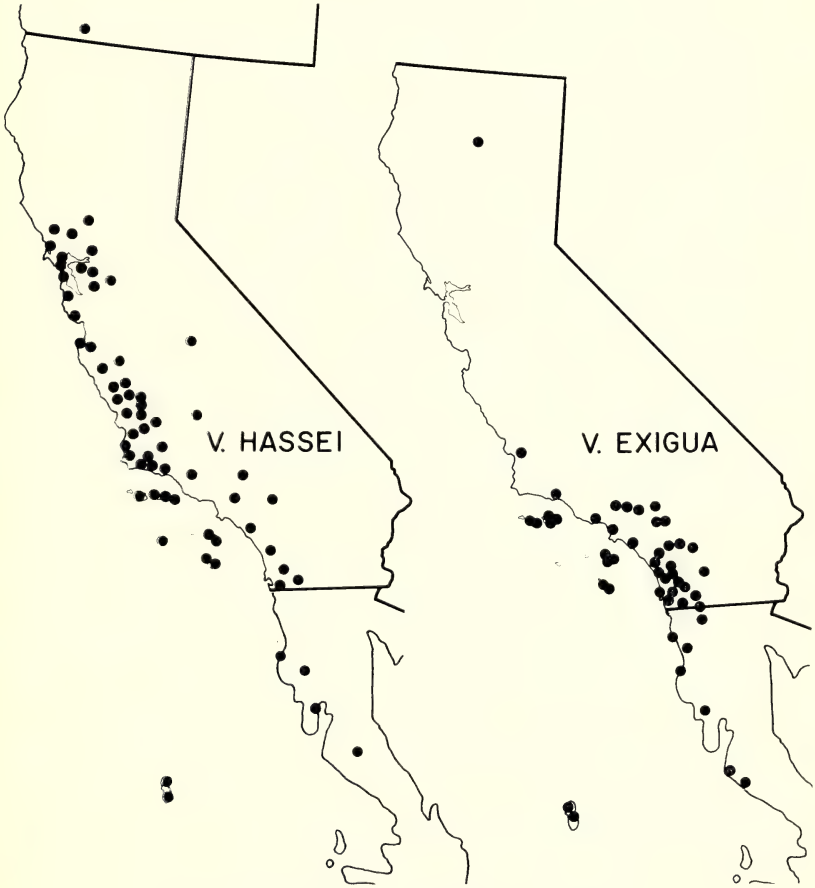

FIG. 3. Distribution of *V. hassei* and *V. exigua*.

Conclusions and Taxonomic Treatment

On the basis of the aforementioned morphological, karyotypic, and distributional differences, I believe it most realistic to consider these taxa as separate species.

Vicia hassei S. Wats., Proc. Amer. Acad. Arts 25:129. 1890.—*Vicia exigua* Nutt. var. *hassei* (S. Wats.) Jeps., Fl. W. Mid. Calif. 296. 1901. Watson examined and cited several specimens from different collectors to formalize a species concept of *V. hassei*. From his cited material that I examined, I designate as Lectotype: hills about Los Angeles with *V. exigua, H. E. Hasse s.n.,* 1888 (GH!). Other cited specimens that I examined are: Santa Cruz, *C. L. Anderson s.n.* (Syntype GH! Isosyntype PH!); Benecia, *Bigelow s.n.* (Syntype GH! Isosyntype NY!).

Vicia exigua Nutt. var. ?*californica* Torr., Pacific Railroad Reports 4:76 1856. Type: Benicia, *Bigelow s.n.* (the same collection cited by Watson for *V. hassei*). Holotype GH! Isotype NY!.

Herbaceous annual, usually robust, but sometimes flowering when less than 10 cm tall, short and stubby-branched to 60 cm or more tall and climbing. Leaflets (2) 4–8 (12), (1.5) 2.0–6.0 (9.0) mm wide and (8.0) 14.2–27.1 (40.0) mm long, the length-width ratio (1.9) 3.2–7.1 (9.0), the apices usually truncate to retuse or emarginate, often with more than one mucro. Flowers 1–2, arising at separate points on the peduncle, white to faint bluish or lavender, the length from calyx base to the tip of the unreflexed standard (6.2) 6.7–7.9 (8.8) mm, calyx teeth subequal, about 1.0 mm long or less, about half or less the length of the calyx tube, the tube (1.6) 2.0–2.6 (2.9) mm long. Stylar pubescence a dense mass, obviously concentrated on the lower side, the hairs 0.25–0.45 mm long. Mature legumes 24–38 mm long, saber-shaped at the tip, the tip curved upward, the internode between two legumes great, 13.0–26.0 mm long. Ovules up to 10.

Distribution: Southern Oregon to Baja California, near the coast and on some offshore islands (fig. 3). Lower elevations and near sea level, often among undergrowth and brush, grassy hills and slopes; canyons, arroyos, and ravines; creeks and flood plains; forest margins; only occasional on rights-of-way. In sandy to rocky and "dry-bog" clay soils. Flowering in March-April, fruiting in April-May.

Vicia exigua Nutt. in T. & G., Fl. N. Amer. 1:272. 1838.—*Cracca exigua* (Nutt. in T. & G.) Alefeld, Bonplandia 9:119. 1861. Type: Columbia plains, *Nuttall s.n.,* (Isotype PH!). The holotype of *V. exigua* (BM) was collected by Nuttall from "the Columbia Plains", but was not available for this study. A photograph was seen, however, and the type sheet contains two specimens. Howell in 1935 expressed some doubt as to the collection site of each specimen by the following note attached to the type sheet:

From the type description of *Vicia exigua* Nutt. (T. & G., Fl. N. A. 1:272) it is obvious Nuttall saw plants from California as well as from the Columbia. I believe that the two specimens on this sheet are from these two regions and that the California label has been lost. From the type description it is easy to determine that the left-hand specimen is the one from "the Oregon," the one on the right from "Upper California." 8/26/35 John Thomas Howell.

The right-hand specimen is definitely *V. exigua,* and I here designate it the lectotype. If this specimen were in fact collected from the Columbia Plains (Oregon) or even from northern California, as Howell believes, it must rank with Eastwood's Shasta Co. collection of *V. exigua* as an outlier from the more common southern California locations. From the type photograph, I cannot positively identify the left-hand specimen.

Herbaceous annual, diminutive to robust, 16–110 cm tall, sprawling to erect, climbing if support is available. Leaflets (4) 6–9 (12), (0.9) 1.6–3.4 (6.3) mm wide, and (9.0) 12.0–25.0 (37.0) mm long, the length-width ratio (3.6) 5.8–11.2 (16.4), the apices acute to truncate. Flowers 1–3, rarely 4, occurring singly at points on the peduncle (but almost contiguous), or 2 flowers arising from the same point, bluish, the length of the flower from calyx base to the tip of the unreflexed standard (4.3) 4.4–6.5 (7.5) mm. Upper calyx teeth usually slightly shorter than the lowest tooth, the lowest tooth (0.9) 1.1–1.5 (1.7) mm long, usually more than half the length of the calyx tube, the tube (1.3) 1.6–2.0 (2.2) mm long. Stylar pubescence more or less evenly distributed around the style, the hairs 0.08–0.15 mm long. Mature legumes 15–26 mm long, oblique at both ends, the 2 or more legumes contiguous or nearly so. Ovules up to 7.

Distribution: Southern California and Baja California; one distant collection from northern California seen (fig. 3). Wooded areas; moist slopes, ravines, and canyons; foothills; along creeks; chaparral; beaches; dry wasteland. Sandy to rocky soil. Flowering in (February-March) April-May; fruiting in (February) April-May (June).

Acknowledgments

I express sincere gratitude to Dr. Duane Isely for his suggestion of the initial dissertation problem and his guidance throughout this study, which represents a portion of a dissertation submitted as partial fulfillment of the requirements for the Degree of Doctor of Philosophy in Botany, Iowa State University, Ames, 1972. Journal Paper No. J-7850 of the Iowa Agriculture and Home Economics Experiment Station, Ames, Iowa. Project 1814. The facilities of the Iowa State Herbarium, supported by the Science and Humanities Research Institute, were used in the preparation of this paper. The Iowa State University Agriculture and Home Economics Experiment Station provided funds for laboratory supplies and some field travel. Field work was supported by N. S. F. Grant GB-27935. Appreciation is extended to the curators of the herbaria mentioned herein

for their courtesy in arranging loans and in permitting my examination of specimens, and to Clare B. Hardham and the late Ernest C. Twisslemann for allowing examination of their personal collections. Ingrid Marin collected viable *V. exigua* seed from Riverside Co., California.

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Correction of the Geographic Distribution of Rhus microphylla (Anacardiaceae).—Barkley (Ann. Missouri Bot. Gard. 24:256–500. 1937) in his monograph of North American *Rhus* included a distribution map (pg. 388) of *Rhus microphylla* Engelm. ex Gray showing its geographic distribution as including Cedros Island and Puerto San Bartolome, Baja California, Mexico. Cedros Island and the adjacent coast were also shown as localitites for *R. microphylla* by Shreve and Wiggins (*Vegetation and flora of the Sonoran Desert,* Stanford Univ. Press. 1964) and Hastings, Turner, and Warren (*An atlas of some plant distributions in the Sonoran Desert,* Univ. of Arizona. 1972). Hastings et al. pointed out that this rather formidable disjunction is puzzling, since *R. microphylla* is primarily a Chihuahuan Desert species, and that they had not seen specimens from either locality.

In spring 1972 and 1973 I specifically searched for *R. microphylla* on Cedros Island in areas that seemed suitable for its growth. I was unable to locate it, but in all these areas there was an abundance of *Pachycormus discolor* var. *veatchiana* (Kell.) Gentry. Curiously, the disjunct localities reported for *R. microphylla* in the Sonoran Desert fall within the known distribution of *P. discolor* var. *veatchiana*. Because of this and the superficial resemblance of these two species, I borrowed specimens (Cedros Island, 8 Dec 1888, *Pond s. n.,* and Port San Bartolome, 27 Nov 1889, *Pond s. n.*) from the University of Notre Dame on which this distribution of *R. microphylla* is based. Although both specimens are sterile branches, they are easily recognized as *P. discolor* and not *R. microphylla,* since the leaves are borne in fascicles (Kellogg, Proc. Calif. Acad. Sci. 2:24. 1860). Also, on the specimen from Cedros Island there is a card written by Lt. Pond stating, "low shrubby bush 18 inches high, four feet across, branching at the ground into four stems, two inches each in diameter, bark peeling, single stem from a tree like above six feet high, six inches thick." The thick stem and peeling bark are both characteristic of *P. discolor* but not *R. microphylla*. I have annotated these specimens as *Pachycormus discolor* var. *veatchiana*. Oddly, they were not annotated by Barkley as *R. microphylla*. *Rhus microphylla* is restricted to the southwestern United States and northern mainland Mexico, but it does not occur in Baja California. I thank Dr. T. Crovello of ND for the loan of the *Pachycormus* specimens.—David A. Young, Rancho Santa Ana Botanic Garden, Claremont, California 91711.

NEW TAXA OF PALAFOXIA (ASTERACEAE: HELENIEAE)

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During preparation of a monograph of *Palafoxia,* we discovered new taxa that are confined to the deserts of southwestern United States and Mexico, typically in sandy soils at low elevations.

Palafoxia arida B. L. Turner & M. I. Morris, sp. nov. Herbae annuae 10–70 cm altae; caules erecti saepe omnino divaricate ramosi scabrosi vel aspero-hispidi raro fere glabri caulibus superis saepe conspice pubescentibus trichomatibus glandularibus. Folia mediocaulina linearia vel lancei-linearia 20–100 mm longa 2–8 mm lata apice gradatim angustata utrinque canescenti-scabrosa; petioli mediocaulini 5–20 mm longi. Capitulescentia subcorymbose cymosa. Capitula 5–40 subturbinata vel fere cylindrica 5–10 mm diametro 20–28 mm alta (floribus exsertis inclusis) 9–20-flora; pedunculi 1–5(7) cm longi; phyllaria principales (6) 7–15 linearia 10–20 mm longa 1–2 mm lata scabra vel dense glandulosi-pubescentia saepe dorsaliter aliquantum carinata. Flores centrales actinomorphi; corolla 9–11 mm longa rosei-alba vel rosea tubis 2–4 mm longis faucibus cylindraceis 6–8 mm longis lobis 1–2 mm longis; rami styli 4–5 mm longi. Achenia linearia 10–15 mm longa faciebus 4 dense vel sparse adpressi-pubescentibus; pappi squamae costis prominentibus; achenia intima supra angulos squamis 4 linearibus acutis 8–12 mm longis supra facies squamis 4 brevioribus abortivis; achenia extima squamis 3–8 inaequales vel nullis. Chromosomatum numerus, $n = 12$.

Type: United States, California, San Bernardino Co., "The Needles", 7 May 1884, *M. E. Jones 3849*. Holotype: US! Isotypes: ARIZ! CAS! DS! F! NY! UC!.

The following voucher specimens, which are deposited in TEX, have a chromosome number of $n = 12$: Arizona, Mohave Co., *Turner 4787;* California, Riverside Co., *Powell* & *Sikes 1383;* and Mexico, Baja California, *Powell* & *Turner 1705*.

Palafoxia arida is named for the arid climate in which it grows. The species is widespread in sandy soils throughout the Mojave, Colorado, and Sonoran deserts of southwestern United States and Mexico.

Recent taxonomists (Munz, P. A. 1959. *A California flora.*) have referred to this species as *Palafoxia linearis*. Nevertheless, this name applies to a related, allopatric taxon occupying coastal sand dunes of southern Baja California. *Palafoxia arida* can be easily distinguished from *P. linearis* in that plants of the former are erect tap-rooted annuals possessing linear-lanceolate leaves with acute apices, whereas plants of the latter are suffruticose, sprawling shrublets having linear leaves with round or obtuse apices.

Palafoxia arida var. **gigantea** (M. E. Jones) B. L. Turner & M. I. Morris, comb. nov. *Palafoxia linearis* (Cav.) Lag. var. *gigantea* M. E. Jones, Contr. W. Bot. 18:79. 1933.

TYPE: United States, California, Imperial Co., sand dunes, W of Yuma, 24 Sep 1931, *M. E. Jones 28599*. Holotype: POM! Isotypes: MO! UC!.

Palafoxia arida var. *gigantea* can be distinguished by its more robust habit (ca 0.9–1.5 m tall), primary stems 0.5–1.0 cm thick, and heads 28–35 mm long. Variety *gigantea* is endemic to the dunes of southeastern Imperial County, California (just west of Yuma, Arizona).

Palafoxia linearis (Cav.) Lag. var. **glandulosa** B. L. Turner & M. I. Morris, var. nov. A *P. linearis* var. *linearis* caulibus foliisque scabrosissimis glandulari-pubescentibus; pappi squamis abortivis brevioribus differt.

Plants perennial, 40–80 cm high, up to 150 cm across; stems suffruticose and branched from the base, forming conspicuous clumps, rather evenly pubescent with stiff, appressed white hairs, densely covered with rough glandular pubescence; leaves simple, succulent, alternate; mid-stem leaves lance-linear to nearly obovate, 25–50 mm long, 3–8 mm wide, with petioles 3–8 mm long, blades rather abruptly terminated by an obtuse or rounded apex (very rarely nearly acute), canescent-scabrous on both surfaces, with dense covering of glandular pubescence; inflorescence a subcorymbose cyme with 3–15(20) heads; heads subturbinate to nearly cylindric, 5–10 mm across, 20–22 mm high (including the projecting flowers), 10–20 flowered, on peduncles 1.5–5.0 cm long; principal phyllaries 8–14, linear, 10–15 mm long, 1–2 mm wide, scabrous-pubescent, especially below (rarely somewhat glandular); florets "white with faint tinge of magenta-pink" on lobes, regular (outer florets becoming zygomorphic); corolla 7–10 mm long, tube 2–3 mm long, throat cylindric (in outer florets somewhat flaring), 5–7 mm long, the lobes 1–2 mm long; style branches 4–5 mm long; achenes 7–11 mm long, linear, 4-sided, densely appressed-pubescent; pappus scales 4–8, unequal, with pronounced midribs, the inner florets normally with 4 linear, acute scales, 6–9 mm long, on the angles, these alternating with 4, much shorter, abortive scales. Chromosome number not determined.

TYPE: Mexico, Baja California, mouth of arroyo along beach at Barril, 48 mi E of Pozo Aleman, 2 Mar 1935, *Ira L. Wiggins 7825*. Holotype: DS! Isotypes: F! GH! UC! US!.

Palafoxia linearis var. *glandulosa* is named for the rough glandular pubescence that densely covers the leaves and mid-stems, a characteristic that distinguishes it from var. *linearis*, which lacks glandular trichomes on these parts. The taxon is restricted to coastal sand dunes of eastern Baja California from latitude 26°30′ N to 29°30′ N while var. *linearis* occupies similar but more southern sites.

We acknowledge, with thanks, Professor M. C. Johnston for providing the Latin descriptions. This paper was supported by N.S.F. grant 29576X.

SPONTANEOUS HYBRIDS IN DODECATHEON (PRIMULACEAE)

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When geographically distinct species grow in unusually close proximity, interspecific hybridization may occur and a hybrid swarm may be produced. This appears to be occurring with two species of *Dodecatheon* on Table Mountain in Butte County, California. One of these, *D. clevelandii* Greene ssp. *patulum* (Greene) H. J. Thomps. is growing out of its usual elevational range, very near a population of *D. hendersonii* Gray ssp. *parvifolium* (Kunth) H. J. Thomps. Certain plants in the *D. clevelandii* population are of unusual morphology and coloration for this species and are hypothesized by the author to be hybrids. In his review of *Dodecatheon,* Thompson (1953) included an analysis of artificial interspecific hybridization. He demonstrated that a cross producing vigorous hybrids is possible between these two species.

A relatively high degree of morphological similarity between two species, as is exhibited by *D. hendersonii* and *D. clevelandii,* may make morphological investigation alone inadequate for delineation of taxa, including hybrids. This study has utilized chromatography in addition to morphology in analyzing putative hybrids and their parentage.

Materials and Methods

The study site is located on Table Mountain, 5.1 km northeast of Cherokee Road from its intersection with Table Mountain Road in Oroville, Butte County, California. Two distinct habitats are represented by an open, grassy pasture adjoining an oak woodland. *Dodecatheon clevelandii* (ca 300 plants) grows in the meadow, in full sun. At this site, it is out of its usual elevational range; it is normally confined to grassy meadows on the Sacramento Valley floor (ca 67 m), whereas on Table Mountain it is found at a much higher elevation (ca 260 m). At this site, *D. hendersonii* (ca 200 plants) is confined to the more shady oak woodland, which is its normal habitat. The putative hybrids are found within the *D. clevelandii* population and near the ecotone area, also in full sun. Other populations of these two species were also studied in Butte County for morphological and chemical comparison with the Table Mountain plants (see Goodwin, 1973).

Morphological analyses were made of approximately 30 plants of each species and of nine of the dozen or so putative hybrids found during the study. Putative hybrids are designated A, B, C, 1a, 1b, 2a, 2b, 3, 4, 6, and 7. Chromosome counts for the two species (four plants each) were made from propiono-carmine squashes of anthers fixed in ethanol:acetic acid

(3:1, v:v). These slides were made permanent and have been retained by the author. Fresh pollen from ten plants of each species and six putative hybrids was subjected to aniline blue-lactophenol stain to indicate percentage of presumably viable pollen; 500 pollen grains per plant were counted. Hauser and Morrison (1964) note that results of this technique tend to give results of slightly higher percentages than the nitro-blue tetrazolium technique they employed, and which they feel to be more accurate. However, the differences in the results of these two techniques were consistently small in their work, and the aniline blue-lactophenol technique was chosen because of its simplicity. Voucher specimens for this study have been deposited in the herbarium of California State University, Chico.

Thin-layer chromatography was used to separate compounds in leaf extracts. Dried leaves from pressed plants were soaked for 18–24 hours in methanol with 0.5 percent HCl. This extract was spotted on silica gel thin layers (SilicAR TLC - 7G, Mallinckrodt). Chromatographs were developed with solvents in two phases: the first phase consisted of t-butanol, acetic acid, and water (3:2:2, v:v). The second phase consisted of acetic acid and n-propanol (1:3, v:v). Each phase was run for 10 cm. Plates were dried, and then exposed to ultraviolet light to make non-pigmented spots fluoresce; they were then treated with ammonia vapor and again exposed to ultraviolet light.

Results

Morphological characteristics of both species and the putative hybrids are summarized in Table 1. Morphologically, all *D. clevelandii* populations studied were very similar. Individuals with pink-tipped corollas were very rare (only three were found in the entire study) and resembled the individuals with white corollas in all other respects. The *D. hendersonii* populations were also very similar, with the exception of corolla coloration. Some populations had a high frequency of the darker magenta color, while others had more individuals with the lavender coloration. Only one totally white individual was found during this study; this plant resembled other plants in that population in all other respects. Putative hybrid plants were distinguished by their pink and white corollas, the condition of the maroon band on the corolla tube, and the absence of the yellow anther dot (see Table 1). No individuals in any *D. hendersonii* population showed the two-toned corolla coloration and maroon band found in the putative hybrids, and no individuals in any *D. clevelandii* population studied showed the absence of the yellow anther dot. For these reasons, the putative hybrids were rather easy to distinguish once they had flowered. Morphological variation of the Table Mountain plants is summarized in Figure 1.

Chromosome counts of both species established that plants with a haploid number of $n = 22$ are present in both species at the Table Moun-

TABLE 1. MORPHOLOGICAL COMPARISONS OF TWO SPECIES OF DODECATHEON AND PUTATIVE HYBRIDS. Samples for the species came from several populations in Butte County (see Goodwin, 1973, for localities).

Character	*D. hendersonii*	*D. clevelandii*	Putative hybrids
Scape height	10–31 cm, avg. 18.4	6–14 cm, avg. 9.7	8.5–18.5 cm, avg. 11.9
Leaf morphology	Spatulate to elliptic	Spatulate to oblanceolate	Variable; tends to resemble *D. clevelandii*
No. flowers per umbel	1–7, avg. 3.9	1–4, avg. 2.2	1–3, avg. 1.9
Corolla-segment coloration	Lavender to magenta, rarely white	White to cream, rarely pink-tipped	Pink-tipped to almost totally pink
Nature of maroon band on corolla-tube	Indented, pointing toward anthers; narrow	Indented, away from anthers; wide	Indented, away from anthers; variable width
Filament-tube width with respect to anther whorl	Narrower	Equally wide	Variable
Yellow dot at base of anthers	Absent	Present	Absent

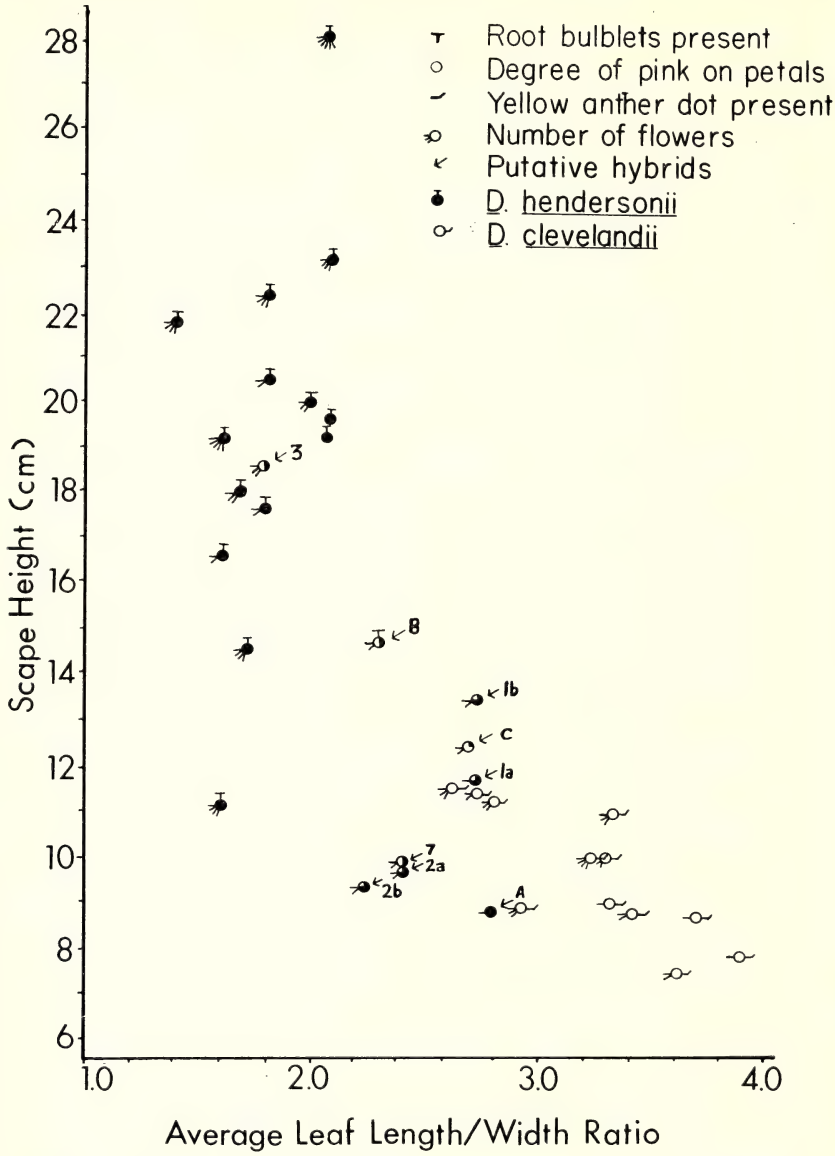


FIG. 1. Scatter diagram of population of *Dodecatheon* at the Table Mountain study site. Root bulblet data were not available for the putative hybrids other than plants A, B, and C, since measurements were made on living plants. Plants A, B, and C represent earlier collections, for which chromatographic data are not available.

tain site. This is in accordance with Thompson's (1953) work on this genus. It was not necessary for this study to establish that all plants of each species had $n = 22$; it was necessary only to establish that such

individuals were present at the Table Mountain site, since hybridization producing viable offspring is possible in this genus only between plants with the same chromosome number (Thompson, 1953).

Pollen stainabilities indicate that both species are highly fertile. *Dodecatheon hendersonii* was consistently high, with an average of 98.8 percent (SD ± 0.66), while *D. clevelandii* was somewhat lower and more variable (average 90.5 percent; SD ± 7.2). Percent stainabilities for the putative hybrids were 58 (plant 1a), 63 (1b), 8 (2a), 8 (2b), 82 (3), and 87 (7). Plants 4 and 6 were not sampled in this respect. These results correlate well with the observed frequency of collapsed or abortive grains.

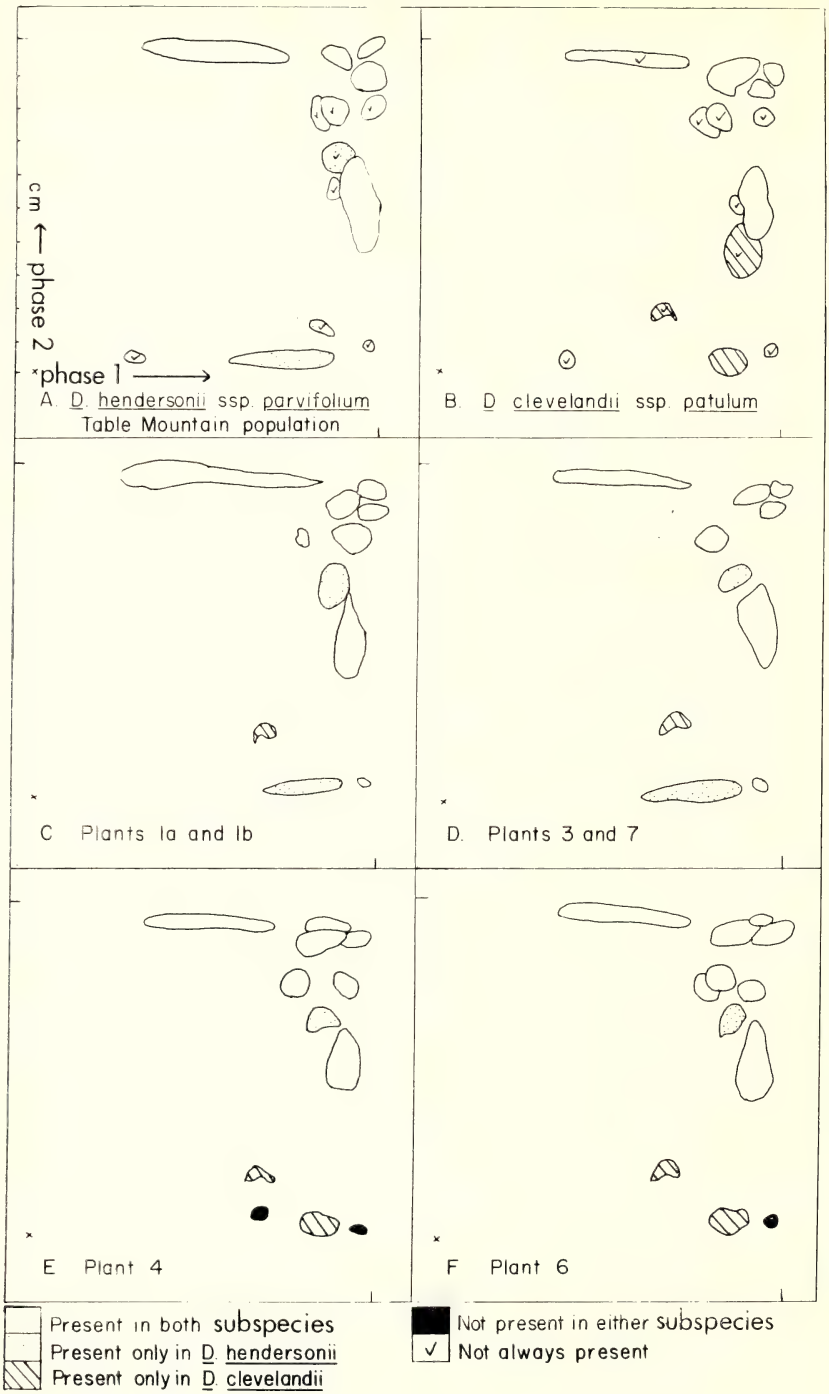
Drawings of chromatographs are shown in Figure 2. Some spots were consistently present for both species, some consistently present for just one species, and some were inconsistent, both in their presence and their species specificity. Some spots were pigmented, while others were visible only under ultraviolet light. For technical reasons, chromatographic data are not available for putative hybrids A, B, C, 2a, and 2b, nor morphological data for plants 4 and 6.

Discussion

In general, the putative hybrids tend to resemble *D. clevelandii* more than *D. hendersonii*, especially with regard to scape height and leaf shape (fig. 1).

Dodecatheon hendersonii and *D. clevelandii* have high pollen stainability and, hence, presumably high viability. They would not, therefore, be expected to have arisen recently as a result of hybridization. Putative hybrids, however, have significantly lower percentages, which supports the hypothesis of hybridization. Plants 1a and 1b, because of their similar morphology and adjacent growing sites, are thought to represent a clone, as do plants 2a and 2b. Pollen stainability results indicate that this is indeed the case. The similar results for each pair would indicate a genetic basis for the sterility, as would be expected in hybrid plants, rather than environmentally induced sterility (frost, nutrition, etc.).

Results of chromatography show that these two species have similar chromatographic profiles (fig. 2, A and B). There are a few species-specific compounds, but the majority of the compounds are shared by both, indicating that these species are closely related genetically. *Dodecatheon hendersonii* was found to be more variable between populations with regard to leaf compounds than was *D. clevelandii*, which was quite consistent chemically between populations. This may indicate a greater degree of genetic heterogeneity among populations of *D. hendersonii* in Butte County. Chromatographs of all the putative hybrids tested (fig. 2, C–F) showed the presence of at least one species specific compound from each species, in addition to compounds found in common with both species. The most probable way that these plants could have received such a combination of compounds is through hybridization between the two species. One of the species-specific compounds of *D. clevelandii* does not


cm ← phase 2
×phase 1 →
A. D. hendersonii ssp. parvifolium
Table Mountain population
B. D clevelandii ssp. patulum
C Plants Ia and Ib
D. Plants 3 and 7
E Plant 4
F Plant 6
Present in both subspecies
Present only in D. hendersonii
Present only in D. clevelandii
Not present in either subspecies
✓ Not always present

show up in any of the hybrids (fig. 2); this may indicate that the genes coding for this substance need to be present in a homozygous condition in order for this chemical to be produced.

Some putative hybrids (fig. 2, E and F) showed the presence of compounds that were not found in either species. Alston and Turner (1963) showed the presence of *de novo* substances in hybrids of *Baptisia* (Leguminosae). These substances could be formed by small mutations or new gene combinations that were present in the putative hybrids but were not present in the two species. An alternative explanation is that they are substances that are present in one or the other species, but that they have been altered in some small way (possibly through hybridization) so as to show different chemical properties in the putative hybrids. Since no qualitative chemical analysis was done on any of these compounds, a definite conclusion concerning these particular spots cannot be drawn at this time.

The range of pollen stainabilities, variations in leaf chemistry, and degree of morphological overlap between the putative hybrids and the two species (fig. 1) may indicate that the putative hybrids do not all represent F_1 offspring. Since the majority of the putative hybrids were growing well within the *D. clevelandii* population, it is not unreasonable to suspect that introgression with the *D. clevelandii* parent has been and is occurring. This may explain why the putative hybrids tend to resemble *D. clevelandii* more than *D. hendersonii*.

Acknowledgments

I express my appreciation to Dr. Kingsley Stern for his constant encouragement and support during the preparation of this paper. This report is excerpted from a thesis submitted to the faculty of California State University, Chico, in partial fulfillment of the requirements for the Master of Arts degree in botany.

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Fig. 2. Chromatographs of two species of *Dodecatheon* and putative hybrids. Those for the two species are composite chromatographs (2A based on 5 plants; 2B based on 6 plants). In addition, the diagram for *D. hendersonii* is accurate for only the Table Mountain population (that for *D. clevelandii* is accurate for all populations sampled). Diagrams C through F represent single plants, unless otherwise noted. For composition of the solvent phases, refer to text.

TAXONOMIC STATUS OF CORDYLANTHUS (SUBG. DICRANOSTEGIA) ORCUTTIANUS (SCROPHULARIACEAE)

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Asa Gray (1883) described *Cordylanthus orcuttianus,* native to northern Baja California and adjacent California, in a monotypic section, *Dicranostegia.* Pennell (1947) raised the taxon to generic rank. Subsequently, the taxon has received scant attention except for treatment (as a genus) by Wiggins (1964) in his flora of the Sonoran Desert. We examined various aspects of the morphology and cytology of this species in conjunction with similar studies of all species of *Cordylanthus.* These comparative studies of flower and inflorescence, of pollen wall and seed coat patterns as observed with scanning electron microscope, and of chromosome numbers give evidence that this species should be retained in *Cordylanthus,* where it forms one of three subgenera. A taxonomic treatment of one of these three groups, i.e., subg. *Hemistegia,* is complete (Chuang and Heckard, 1973) and an infrageneric classification of subg. *Cordylanthus* that proposes division into sections is in preparation.

Cordylanthus is a member of the subtribe Castilleiinae (tribe Rhinantheae) and stands apart from the other five members *(Castilleia, Orthocarpus, Clevelandia, Ophiocephalus, Gentrya)* of that subtribe (Breedlove and Heckard, 1970) on the basis of its spathe-like, usually bifid calyx.

All members of the subtribe are root-parasites; *C. orcuttianus* is a facultative root-parasite that has been successfully cultivated both with and without a host (Chuang and Heckard, 1971). Data on probable natural hosts of *C. orcuttianus* are meager but the plants are characteristically found in openings among shrubs and herbaceous perennials that are probable hosts. Whether there is a high degree of host-specificity that limits *Cordylanthus* to the geographic range of one or few hosts is unknown.

Comparative Morphology

Cordylanthus orcuttianus has an indeterminate elongate spike (fig. 1 a), an unspecialized type of inflorescence characteristic of subg. *Hemistegia* and some species of subg. *Cordylanthus.*

The floral bract that subtends each flower of the spike is spathe-like with 1–3 pairs of linear-lanceolate lobes near the middle (fig. 1 c and d)

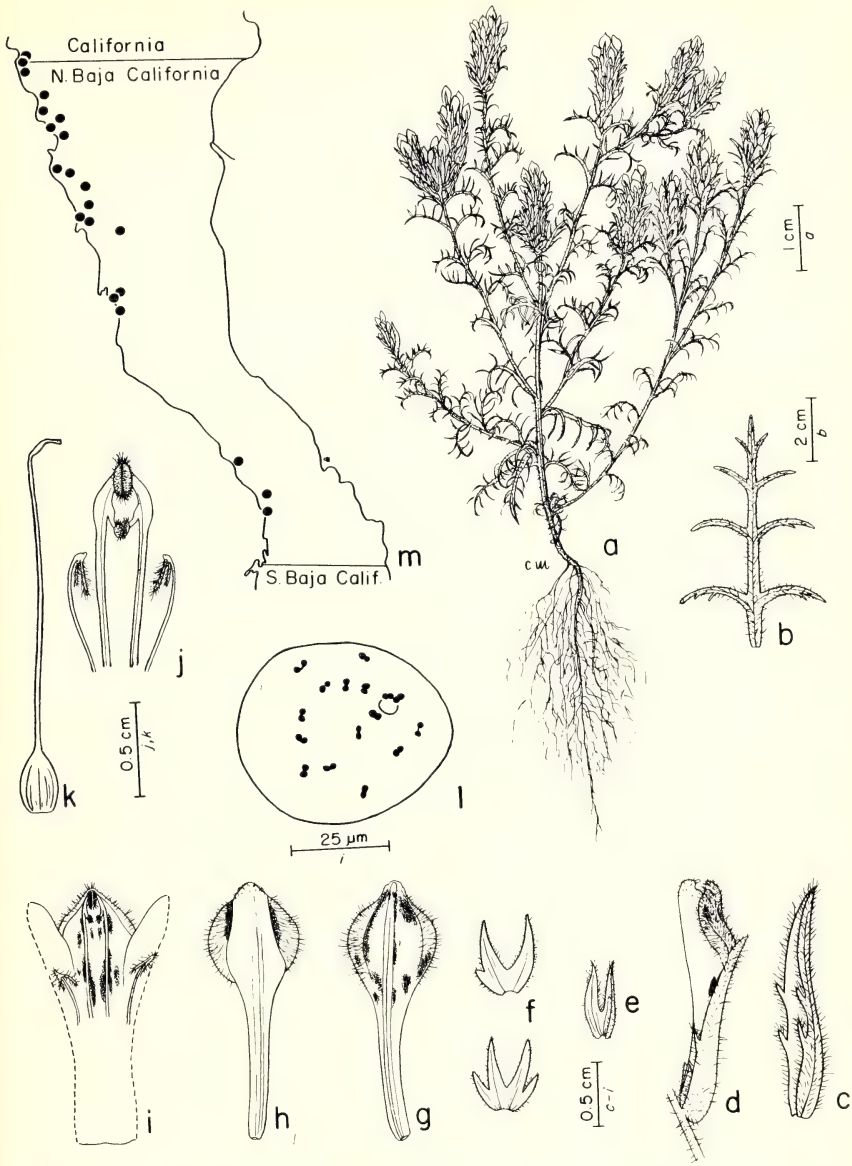


FIG. 1. *Cordylanthus orcuttianus*. a, habit; b, leaf; c, floral bract; d, flower e, calyx; f, variations of calyces; g, ventral view of flower with calyx removed; h, dorsal view of flower with calyx removed; i, flower opened dorsally; j, anthers; k, pistil; l, meiotic chromosome figure, $n=16$, diakinesis; m, distribution map. a–i and k-l from *Moran 15392;* j from *Heckard 3240*. Drawings by Charlotte Mentges.

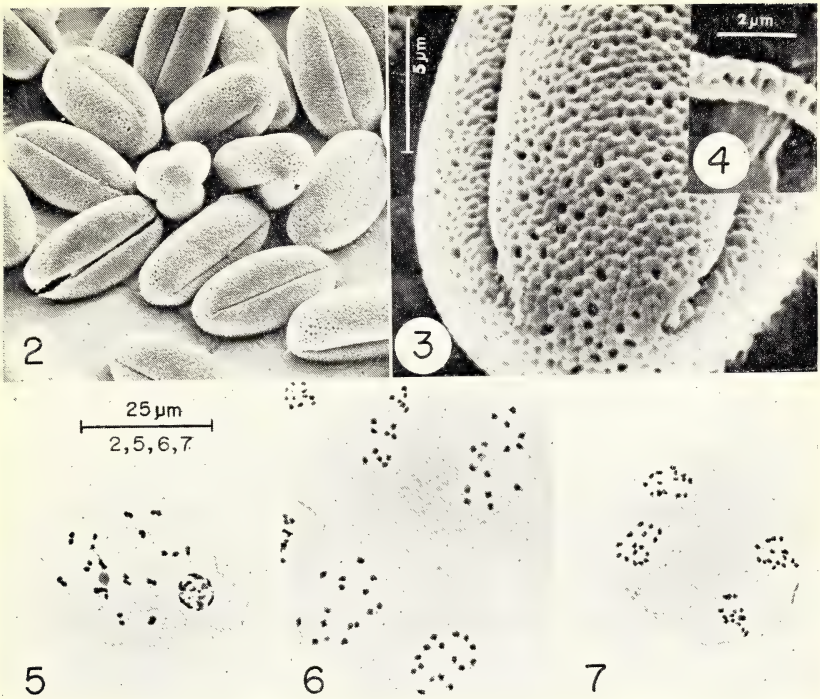
and resembles the bract found in some species of both subg. *Hemistegia* (Chuang and Heckard, 1973) and subg. *Cordylanthus*.

Cordylanthus has a distinctive spathe-like calyx usually about as long as the corolla and slightly bifid at the apex with a 1–2 mm slit or sometimes entire. In *C. orcuttianus*, however, the calyx is smaller (¼ to ⅓ the length of the corolla) and deeply bifid to ⅔ its length, forming two attenuate lobes (fig. 1 d and e). The calyx surrounds the base of the corolla tube dorsally and laterally (fig. 1 d) but does not have a short basal tube as in some species of subg. *Cordylanthus*. Occasional flowers in an inflorescence of some plants raised from seed (*Moran 15,392*, JEPS) develop either 3- or 4-lobed calyces (fig. 1 f). These abnormal calyces have one or two extra, smaller or vestigial, anterior lobes, each of which is supplied with a vein.

The club-shaped corolla of *C. orcuttianus* (fig. 1 g and h) resembles that of other members of *Cordylanthus*. The stamens, however, are variously modified from those in the remainder of the genus. The dorsal pair are sterile, each with two heavily bearded vestigal anther sacs (fig. 1 i and j). Each stamen of the fertile ventral pair has an enlarged and elongated (2 mm) connective forming a slightly curved arm bearing a large anther sac attached medianly at the top of the connective and a smaller sac below at the end of a short spur (fig. 1 i and j), which is almost 1 mm long.

Cordylanthus orcuttianus, like *C. palmatus* (subg. *Hemistegia*), has seed with arching crests on the dorsal side. The seed is cochlidiospermous, 1.0–1.5 mm long with strongly reticulate seed coat and irregularly scalariform thickenings on the reticulum surface. Seed coat morphology of *C. orcuttianus* is in most respects similar to that of subg. *Hemistegia,* indicating a possible relationship between the two subgenera (Chuang and Heckard, 1972).

Pollen grains used for this study were obtained from herbarium specimens *(Heckard 3240)*. For light microscopy, pollen samples were acetolyzed (Erdtman, 1960) and mounted in glycerine jelly. For scanning electron microscopy, dried pollen grains and sections were coated with gold under a conventional vacuum evaporator and then were examined and photographed with Cambridge Stereoscan Electron Microscope. For obtaining sections acetolyzed pollen grains were cut at 2–4 μm using a freezing microtome at $-30°$C. The general shape of *C. orcuttianus* pollen is prolate or subprolate in equatorial view, 24–27 $\times$ 17–20 μm, and rounded-triangular in the polar view. Grains are 3-colpate; colpi are long, with tapering ends (fig. 2). The exine is ca 1 μm thick and its surface is microreticulate and not uniformly perforate (fig. 3). The sexine is made up of bacula supporting the perforate tectum (fig. 4). From our preliminary investigation using SEM, pollen morphology appears to be fairly uniform throughout the genus, with 3-colpate and microreticulate exine.



FIGS. 2–7. Scanning electron micrographs of pollen grains and photomicrographs of chromosomes of *Cordylanthus orcuttianus*. 2. Equatorial and polar views of pollen grains. 3. Oblique view of grain showing unequally perforate tectum. 4. Sporoderm section of pollen grain showing foot layer, bacula, and tectum. FIGS. 5–7. Meiotic chromosome figures, $n = 16$. 5. Diakinesis. 6. Prophase II. 7. Telophase II.

CYTOLOGY

Cordylanthus orcuttianus has $n = 16$ (figs. 1 l, 5, 6, and 7). Meiosis was regular in several aceto-carmine squashes of pollen mother cells fixed in acetic acid-ethanol (1:3, v/v). A sampling was made from several plants raised in the greenhouse from a single general seed collection *(Moran 15,392)*. Other chromosome counts for the genus are $n = 14$, 15, and 21 for subg. *Hemistegia* (Chuang and Heckard, 1973) and $n = 12$, 13, 14 (unpublished data) for subg. *Cordylanthus*. The diversity of chromosome numbers within the genus is a useful adjunct to other information in *Cordylanthus* taxonomy and each number (except $n = 14$) coincides with one particular group of related species.

DISCUSSION AND CONCLUSIONS

Our comparative studies do not support Pennell's view (1947) that *C. orcuttianus* deserves generic status. Basic features setting *Cordylanthus*

apart from its closest relatives in Castilleiinae—namely, the club-shaped corolla and the 2-lobed, one-sided calyx—occur also in *C. orcuttianus*. Seed-coat and pollen-wall features are also similar. The only features consistently different from those in other members of *Cordylanthus* are the deeply pinnately dissected leaves, the smaller and more deeply cleft calyx, the elongated connective that separates pollen sacs of the anther, and the chromosome number, $n = 16$. The only morphological difference mentioned by Pennell was that of the calyx. He also pointed out that the plants flowered in spring while the other species were summer and early fall bloomers. While it is true that *C. orcuttianus* flowers earlier, its flowering period extends also into late summer. *Cordylanthus maritimus* Nutt. ssp. *maritimus* (subg. *Hemistegia*) begins flowering in May, only a month later than for *C. orcuttianus* growing in the vicinity, the Mexican border at Tijuana.

Most morphological differences of *C. orcuttianus* are only variations in degree of features found in other members of the genus. In some instances features of *C. orcuttianus* are most likely primitive in the genus, as in the case of the pinnately dissected leaf and deeply cleft calyx, but the elongated anther-connective and chromosome number of $n = 16$ seem to be derived conditions. Although pinnately dissected leaves are limited to this species in the genus, bracts and upper cauline leaves are shallowly pinnately lobed in *C. mollis* (subg. *Hemistegia*), as are bracts in *C. kingii* (subg. *Cordylanthus*). We interpret the pinnately dissected leaf as primitive in Castilleiinae, since it is found in presumably primitive species of *Castilleia* (Holmgren, 1971) and *Orthocarpus*. We agree with Pennell (1947) that the calyx of *C. orcuttianus* is less modified than that of other species in the genus, which have extensive fusion of the two lateral lobes. The apex of the clyx is deeply divided only in *C. orcuttianus* and, about half as far, in *C. capitatus* (subg. *Cordylanthus*).

The calyx of *C. orcuttianus* is completely divided to the base ventrally and ⅔ of its length dorsally (fig. 1 e). We postulate that it evolved by modification of the typical 4-lobed calyx of Castilleiinae. Such a 2-lobed calyx could arise by division of the tube ventrally and fusion of each pair of lobes to form only two lobes. The abnormal 4-lobed calyx (fig. 1 f) seen in greenhouse plants and described earlier may evidence a 4-lobed stage in evolution of the *Cordylanthus* calyx. Pennell (1947) postulated development of the calyx in much the same way and believed that further evolution uniting the lobes dorsally and elongating them wholly on the upper side formed the calyx found in the rest of the genus. He suggested that the resultant calyx was so different that the two types could not satisfactorily be included within the same genus. We see them, however, as basically the same type of calyx, representing different stages in evolution of the completely united spathe-like calyx.

The elongated connective of the anther (fig. 1 j) was not mentioned by Pennell (1947) but is a novel feature of the species and undoubtedly

is a modification of the condition in Castilleiinae in which the small connective bears two unequal anther sacs, a large one attached medianly and a smaller one attached apically. In the functional stamens of *C. orcuttianus,* the anthers are unequal in size but the connective is considerably enlarged, resulting in a strikingly modified stamen. Reduction of the dorsal stamens has occurred independently in all three subgenera.

Although the chromosome number, $n = 16$, of *C. orcuttianus* is unique in the genus, differences in chromosome number are not necessarily evidence of generic separation. All numbers from $n = 12$ to 16 (plus 21) are found in *Cordylanthus*.

Taxonomy

Cordylanthus Nutt. ex Benth. subg. **Dicranostegia** (A. Gray) Chuang & Heckard, stat. nov.—*Cordylanthus* sect. *Dicranostegia* A. Gray, Proc. Amer. Acad. Arts 19:95. 1883.—*Adenostegia* sect. *Dicranostegia* (A. Gray) Ferris, Bull. Torrey Bot. Club 45:417. 1918.—*Dicranostegia* (A. Gray) Pennell, Proc. Acad. Nat. Sci. Philadelphia 99:189. 1947.—Type species: *Cordylanthus orcuttianus* Gray.

Plants of coastal and desert scrub communities. Leaves deeply pinnately dissected with linear lobes. Inflorescence a dense spike. Floral bracts oblong-lanceolate with 1–3 pairs of pinnately arranged linear lobes. Calyx short, less than ½ as long as corolla, deeply divided into two attenuate lobes, surrounding only the lower corolla tube dorsally and laterally. Stamens 4, the ventral pair fertile with elongated connective bearing 1 anther sac at either extremity; the dorsal pair sterile with aborted anther sacs. Seed deeply reticulate.

Cordylanthus orcuttianus A. Gray, Proc. Amer. Acad. Arts 19:95. 1883.—*Adenostegia orcuttiana* (A. Gray) Greene, Pittonia 2:181. 1891.—*Dicranostegia orcuttiana* (A. Gray) Pennell, Proc. Acad. Nat. Sci. Philadelphia 99:190. 1947.—Type: Mexico: Baja Calif., "about 70 miles below the U.S. boundary, H. C. Orcutt and son". (Holotype: GH!; isotype: K!) Identity of the type specimen of *C. orcuttianus* is questionable, perhaps due to a labeling error. Although Gray (1883) described the type locality as "70 miles south of the border", the only collection seen by us that was made by H. C. Orcutt and son prior to the 1883 publication date is one labeled as "Tia Juana Lower Calif., 1883, H. C. Orcutt & Son" (GH!). The two unusually small plants agree with Gray's description of the plants as "only 6 inches high, mostly branched from the base". A single, similar plant with the label (probably in Gray's hand) "Lower California, Orcutt, 1883—Ex Herb. A. Gray 1/1884" is at K(!). No specimen from "70 miles south of the border" was found, indicating to us that the 1883 collection is the type and that it was labeled rather casually (or erroneously) as from "Tia Juana".

Annuals 20–35 (10–50) cm tall, divaricately branched mostly from near the base with several to many ascending or decumbent branches; herbage green or often suffused with dark red, densely to sparsely hirsute. Leaves 3–6 (2–8) cm long and 3–5 cm broad, pinnately dissected with 4–5 pairs of linear to subulate segments 1.0–1.5 mm broad, rachis up to 3.5 mm broad, occasional lower segments slightly lobed. Inflorescences of dense spikes 2–10 cm long, 2–3 cm broad, subtended by outer bracts. Floral bracts 1.5–2.5 cm long, oblong-lanceolate with 1–3 pairs of linear ascending lobes 0.5–1.5 cm long, 3-veined, hirsute along margins and veins. Calyx ca 6 mm long, divided to over ½ its length into 2 attenuate lobes ca 4 mm long, occasionally forming 4 or 3 lobes with lateral ones smaller, each lobe 3-veined, hirsute along margins and veins, the base of calyx partially surrounding the base of corolla tube dorsally and laterally. Corolla club-shaped, two-lipped, 1.8–2.5 cm long, exceeding the floral bracts, the tube slightly exceeding the throat, white with lips yellow-tipped, the throat conspicuously inflated laterally, ca 6 mm broad; upper lip galeate and rounded apically with lateral margins enclosing the style and coherent anthers; lower lips 4 mm long, with dark red margins and scattered flecks of dark red extending back along the white throat; galea puberulous dorsally, the lower lip and throat velutinous. Stamens 4, didynamous, ventral pair fertile with elongated connective forming a bent arm bearing one anther sac at either extremity, the upper anther sac larger, ca 1.2 mm long, hirsute at both ends; lower sac smaller, ca 0.5 mm long, densely hirsute; upper pair of stamens sterile, the vestigial anther sacs represented by two hyaline, villous appendages; filaments glabrous; style elongate, the tip bending downward and emerging through apical notch in galea, the stigma barely exposed. Seeds dark brown, 1.0–1.5 mm long, irregularly reniform, deeply reticulate with conspicuous arching crest on dorsal side, 32–40 in each capsule. Chromosome number $n = 16$.

Habitat and Distribution (fig. 1 m): Along sandy arroyos, washes, and on slopes and plains in openings among shrubs, as *Ambrosia, Atriplex, Virguieria, Bebbia,* and *Solanum;* largely coastal, just north of United States border in San Diego County, California, and in N Baja California of Mexico south to the vicinity of Miller's Landing, just north of latitude 28°N; sea level to ca 350 m; flowering April to July (March to September).

Representative specimens: United States: California: San Diego Co.: 2 mi E of San Ysidro on Otay Mesa, *Gander 219.21* (SD).

Mexico: Baja California: boundary line near Monument 258P, *Mearns 3927* (DS); S of Tijuana, *Pennell & Epling 25200* (CAS, F, NY, PH, UC); 6 mi NE of Descanso, *Wiggins & Thomas 351* (DS); 3 mi E of La Mission. *Moran 13156* (RSA, SD, UC); 2.5 mi NW of San Antonio, *Moran 13948* (DS, SD); Sauzal, *Orcutt & Fish s.n.* (MO, US); Ensenada, *Brandegee s.n.* (UC); Arroyo Santo Tomas, *Wiggins & Thomas 402* (DS); near San Jacinto, *Gander 7308* (SD); S of San Vicente,

Pennell & Epling 25254 (NY, PH, UC); San Antonio del Mar, *Gander 7358* (SD); Colnett, *Moran 13999* (SD); 6.5 mi W of Rancho San José, *Wiggins 10046* (DS, UC); 10 mi E of Santa Margia, *Moran 11011* (SD); 10 mi S of San Quintín, *Harbison 41819* (PH, RSA, SD); El Socorro, *Moran 15392* (ISU, JEPS, SD); 7 mi SW of Punta Prieta, *Heckard et al. 3240* (JEPS, ISU); 5 mi N of Miller's Landing, *Wiggins 5727* (CAS, DS, F, NY, POM, RM, UC).

Acknowledgments

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Salsola soda L. (Chenopodiaceae) in Central California.—This species, sometimes known as Glasswort, is a native of southern Europe, and has become established in several localities around the margins of San Francisco Bay. In some places, as the Palo Alto Yacht Harbor, it is very common. It can be expected to spread in California. The standard floras for California (P. A. Munz', *A California flora,* 1959; *Supplement,* 1968; and *A flora of Southern California,* 1974, all University of California Press, Berkeley) do not record this species nor do two recent papers (J. T. Howell, Miscellaneous notes on Munz' A California flora and Supplement, Wasmann J. Biol. 30:97–107. 1972; J. C. Beatley, Russian-thistle *(Salsola)* species in western United States, J. Range Managem. 26:225–226. 1973). It would appear that *Salsola soda* is a new introduction into western North America and perhaps for the entire continent. Specimens seen so far from California are: Alameda Co.: Alameda, *Long s.n.,* 6 Oct 1971 (CAS); *Long s.n.,* Nov 1971 (CAS). San Mateo Co.: W end Dumbarton Bridge, *Anderson s.n.,* 25 Jul 1968 (CAS); *Anderson s.n.,* 16 Aug 1968 (CAS); *Thomas 14860,* 7 Dec 1968 (DS); Palo Alto Yacht Harbor, *Thomas 17615,* 6 Oct 1974 (DAO, DS, MO, OCS, RSA). Santa Clara Co.: Palo Alto Yacht Harbor, *Thomas 17603,* 22 Sep 1974 (DS, JEPS).—John H. Thomas, Department of Biological Sciences, Stanford University, Stanford, California 94305.

A NEW HYBRID FLESHY-FRUITED PRICKLY-PEAR IN CALIFORNIA

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Only two species of prickly-pear cacti grow in San Luis Obispo County, California. These are *Opuntia phaeacantha* Engelm. var. *major* Engelm. and the Indian-fig cactus, *O. ficus-indica* (L.) Miller *(Opuntia* series *Opuntiae).*

Opuntia phaeacantha var. *major* is widespread in southwestern United States. Its northwesternmost station is at Radio Tower Hill on the campus of California Polytechnic State University. In San Luis Obispo County it is found on south- and/or west-facing slopes near the coast and in Cuyama Valley. All of the populations are morphologically rather uniform.

The spiny form of *Opuntia ficus-indica* ("megacantha" sensu Benson, 1969a) was introduced into California by the mission fathers in the late eighteenth century (Benson and Walkington, 1965). It and the spineless form were planted for their edible fruits and as a source of mucilaginous binding material for adobe bricks. They were planted at missions and rancheros in southern and central California and elsewhere in the Southwest. There are numerous populations in the San Luis Obispo area on hillsides and along water courses; one large clone growing on the southeastern flanks of Mt. San Luis Obispo is apparently an escape from the original mission garden.

Opuntia phaeacantha var. *major* is usually prostrate (occasionally suberect), rarely exceeding 30 cm in height. Stem joints are obovate, averaging about 15 cm long by 11 cm wide. Spines are brown to reddish-brown with white tips and 3.5–7.5 cm long. Fruits are obovoid and wine-colored.

Opuntia ficus-indica "megacantha" is tree-like, 3–5 m tall. Stem joints are obovate or oblong, 30–60 cm long by 20–40 cm wide. Spines are white and 1.0–2.5 cm long. Fruits are nearly spherical and yellow or pale orange.

These two cacti grow in close proximity on steep, west-facing slopes of Hospital Hill in northeastern San Luis Obispo. Three individual plants that are intermediate, for the characters mentioned above (as well as others), between *Opuntia ficus-indica* "megacantha" and *O. phaeacantha* var. *major* were found on this hillside. These intermediates are shrubby to sprawling, about 1.0–1.5 m tall. Stem joints are obovate averaging about 20 cm long by about 15 cm wide. Spines are light yellow, slightly

darker at the base and average 3.0–3.6 cm long. Fruits are obovoid, orange.

Cytological studies (Pinkava and McLeod, 1971; Pinkava et al., 1973) indicate that *O. ficus-indica* is octoploid ($8x = 88$) and that *O. phaeacantha* var. *major* is hexaploid ($6x = 66$). The expected chromosome number of the hybrid between these two taxa is therefore $7x = 77$.

Flower buds for the two putative parental taxa and the intermediate were collected from representative plants from the Hospital Hill population during spring 1974. Acetocarmine squash preparations were made using procedures previously described (Pinkava et al., 1973). Voucher specimens are on deposit in OBI and ASU.

Meiotic chromosome counts were obtained from *O. phaeacantha* var. *major (McLeod 1265)*, $n = 33$, and from *O. ficus-indica* "megacantha" *(McLeod 1255)*, $n = 44$. In the intermediate *(McLeod 1254)*, a prophase II configuration indicated that a 38/39 anaphase I separation had occurred. In a cell at diakinesis, 29 bivalents, one univalent, three tetravalents, and one ring-of-six chromosomes were found ($2n = 77$). This is the first odd-ploid interspecific natural hybrid to be recorded for the Cactaceae.

Walkington (1966) has indicated that *O. oricola* Philbrick of southern California coastal regions may have originated as a hybrid between *O. ficus-indica* "megacantha" and some member of the "*O. phaeacantha* complex". He also suggested that the "*O. demissa*" form found farther inland may have originated through hybridization between *O. phaeacantha* var. *discata* (Griffiths) Benson & Walkington, *O. littoralis* (Engelm.) Cockerell var. *austrocalifornica* Benson & Walkington, and *O. ficus-indica*. Walkington has also stressed hybridization between the naturally occurring cismontane taxa and *O. ficus-indica* in the development of the "*O. littoralis* complex" as it presently exists.

Benson (1969b) postulates the origin of *Opuntia dillei* Griffiths of western Texas and southern New Mexico through hybridization between *O. ficus-indica* and *O. phaeacantha* var. *discata* or var. *major*. I have presented a hybridization scheme for possible origin of the "*O. phaeacantha* complex" of Arizona (McLeod, 1973). Information that crosses such as that of the Hospital Hill intermediate are possible may aid in unravelling taxonomic problems such as these. Cytological studies and a breeding program should yield much additional information regarding these taxa.

Evidence for the origin of the plants from Hospital Hill as a hybrid between *O. phaeacantha* var. *major* and *O. ficus-indica* "megacantha" is summarized as follows: (1) distinct intermediacy of habit, pad size and shape, spine length and color, and fruit size, shape, and color; (2) intermediate chromosome number ($2n = 77$); (3) absence of other prickly-pear species in the vicinity [the nearest being *O. littoralis* var. *littoralis*, 48 km away at northern edge of Santa Maria Valley (Benson, 1969a), although recent observations indicate that Santa Barbara populations

160 km away probably represent the nearest extant populations]. Only three hybrid individuals (most probably first generation progeny) are known; a search of other areas of San Luis Obispo County where the two taxa co-exist has not revealed additional intermediates. Discovery of these natural hybrids could be extremely important in further taxonomic studies of the fleshy-fruited prickly-pears.

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Argemone munita (Papaveraceae): Range Extension and Morphological Notes.—The range of *Argemone munita* Dur. & Hilg. has been extended north and west: California, Trinity County, 8 km NW Stuart Gap on Forest Service Road 28N10, Trinity National Forest, T2S, R11W, sec. 25, 1370 m, 12 June 1973, *Hohn 1085* with Louise Sparks, WTU. A small population was observed on a southeast-facing embankment and roadside ditch. A review of pertinent literature revealed localities for this species along the eastern slopes of the Sierra Nevada north to Shasta County and in the coast ranges to Lake and Colusa Counties, California (G.B. Ownbey, Mem. Torrey Bot. Club 21(1). 1958).

In his monograph, Ownbey stated that *A. munita* is a highly variable species and that precise definition of it is difficult. Four subspecies were described and intermediates (putative hybrids) occur between two of them: subsp. *munita* and subsp. *rotundata* (Rydb.) G. Ownbey. Specimens from localities nearest Trinity County (Shasta County) are intermediate between these two subspecies. Plants from Trinity County are atypical within the morphological limits set for *A. munita* and appear to be aberrant forms unlike any of the described variants or intermediates. A character frequently used in recognizing aberrant forms within the species is the indurated apical spine of the sepal horn. The spine tends to be flattened and enlarged at its juncture with the herbaceous lower part of the horn in plants from the new locality. Such aberrant forms pose taxonomic problems, yet a conservative course in this case is probably the wisest one. In spite of obvious objections, these plants should be assigned provisionally to subsp. *munita* (pers. comm. G.B. Ownbey). Further collection and study of *A. munita* in the Stuart Gap area is desirable.—Janet E. Hohn, Department of Botany, University of Washington, Seattle 98195.

Cytological and Taxonomic Notes on North American Salix.—The following chromosome counts are from pollen mother cells. Vouchers are in RM with duplicates of most in my personal herbarium and in CAN. Counts reported without discussion agree with published reports.

Salix amygdaloides Anderss. $2n = 38$: Wyoming, Laramie Co., Crystal Lake Reservoir, *Dorn 2082*.

Salix athabascensis Raup. $2n = 114$: Alberta, Maskuta Creek near Hinton, *Dorn 1903*. Suda and Argus (Canad. J. Bot. 47:860. 1969) reported counts of $2n = 76$ and $2n = 114$ from the Yukon and Saskatchewan, respectively.

Salix bebbiana Sarg. $2n = 38$: Wyoming, Teton Co., Blacktail Butte, *Dorn 1228*; Alberta, Maskuta Creek near Hinton, *Dorn 1902*.

Salix drummondiana Barratt ex Hook. $2n = 38$: Wyoming, Teton Co., Teton Park, *Dorn 1232*. $2n = 76$: Colorado, Clear Creek Co., Georgetown, *Dorn 1942;* Wyoming, Albany Co., near Centennial, *Dorn 2085, 2234*. The count of $2n = 38$ is from a plant with oblong-lanceolate leaves that are densely silver-pubescent beneath. The counts of $2n = 76$ are from plants with broader leaves and less pubescence. Suda and Argus (Brittonia 20:196. 1968) reported $2n = 57$ for *S. subcoerulea* Piper from Saskatchewan. Argus (Natl. Mus. Canada Publ. Bot. 2:186. 1973) now considers this a synonym of *S. drummondiana*. More counts are clearly needed.

Salix exigua Nutt. $2n = 38$: Wyoming, Laramie Co., Crystal Lake Reservoir, *Dorn 2081*.

Salix geyeriana Anderss. $2n = 38$: Wyoming, Albany Co., Laramie Range, *Dorn 2076*. This is the first count for this species.

Salix lasiandra Benth. var. *caudata* (Nutt.) Sudw. $2n = 76$: Wyoming, Teton Co., Teton Park, *Dorn 1258*. This is the first count for this variety.

Salix lemmonii Bebb. $2n =$ ca. 76: Wyoming, Teton Co., Teton Park, *Dorn 1226*. I originally identified this plant as *S. geyeriana* (Dorn 1974, Ph.D. Thesis, Univ. Wyoming), but the flavonoid profile and morphology both match those of a specimen of "good" *S. lemmonii* from California (*Copeland 620a*, RM). I have not been able to find a morphological character that will always separate *S. lemmonii* from *S. geyeriana*. This is the first count for the species.

Salix ligulifolia Ball ex Schneider. $2n = 38$: Wyoming, Albany Co., Little Laramie River, *Dorn 1755, 1756*. These are the first counts for this species.

Salix maccalliana Rowlee. $2n =$ ca. 214: Alberta, N. Saskatchewan River near Banff Park, *Dorn 1894*. Suda and Argus (Brittonia 20:195. 1968) reported $2n =$ ca. 224 and $2n =$ ca. 190 from Saskatchewan and Alberta, respectively. The actual number is probably $2n = 228$.

Salix planifolia Pursh. $2n = 76$: Wyoming, Albany Co., Dale Creek, *Dorn 1761*; Woods Creek, *Dorn 1865*. $2n =$ ca. 76: Montana, Beaverhead Co., W. Fork Price Creek near Monida, *Dorn 1884, 1885*. Suda and Argus (Brittonia 20:196. 1968) reported four counts of $2n = 76$ and one count of $2n = 57$ all from Saskatchewan and one count (Canad. J. Bot. 47:861. 1969) of $2n = 57$ from the Yukon. Löve and Löve (Taxon 13:202. 1964) reported $2n = 76$ from New Hampshire. None of these counts corresponds to any count for the Eurasian *S. phylicifolia* L. There is now little question of the distinctness of the North American *S. planifolia* from *S. phylicifolia*.

Salix vestita Pursh. $2n = 38$: Alberta, Highwood Summit about 44 miles south of Seebe, *Dorn 1910*.

Salix wolfii Bebb. $2n = 38$: Wyoming, Teton Co., Teton Park, *Dorn 1241*. This is the first count for this species.

This work was part of a doctoral dissertation submitted to the Graduate School of the University of Wyoming and was supported by NSF Grant GB-33470 and a May Duff Walters scholarship from the National Council of State Garden Clubs, Inc.—Robert D. Dorn, Department of Botany, University of Wyoming, Laramie 82071.

New Distribution Records for Montana.—During a study of meadows surrounding Twin Lakes, Bitterroot National Forest, Ravalli County, Montana, ten species that had not previously been recorded for the county (Booth and Wright, *Flora of Montana, part II,* 1959, plus revisions by Booth, 1962, 1966) were found: *Boykinia major* A. Gray var. *major, Hypericum anagalloides* C.&S., *Lonicera caerula* L., *Mitella breweri* A. Gray, *Rhododendron albiflora* Kuntze, *Sambucus melanocarpa* A. Gray, *Saxifraga oregana* Howell var. *oregana, Tiarella unifoliata* Hook., *Vaccinium caespitosum* Michx., *Veronica serpyllifolia* L. Twin Lakes is an irrigation lake system lying in a cirque catchment at ca 2042 m. Vouchers were deposited at MONTU. A checklist indicating abundance and habitat for all species found at Twin Lakes is available from the author. I am grateful to Robert Irving, LeRoy Harvey, Klaus Lackshewitz, and William Gillespie for their help in the project.—Ms. Terry S. Gillespie, Department of Biological Sciences, University of Illinois at Chicago Circle, Box 4348, Chicago 60680.

Collomia tinctoria (Polemoniaceae) in Southern California.—The distribution of *Collomia tinctoria* Kell. in California is well documented for the Sierra Nevada north of Mariposa Co. and the North Coast Ranges north of Lake Co. (Munz, *A California flora,* 1959; Jepson, *A manual of the flowering plants of California,* 1925). The latter treatments do not indicate a distribution in southern California for *Collomia tinctoria* and this species is not treated in Munz's recent text (*A flora of southern California*, 1974). *Collomia tinctoria* does occur in southern California as documented by the following: Santa Barbara Co., near top of San Rafael Pk., *Blakley 4432* (SBBG); saddle on Big Pine Mtn., *Blakley 6042* (SBBG, RSA); "Big Pine Grade" near junction with road to West Big Pine Lookout, *Piehl 63–583* (SBBG); near Madulce Pk., *Piehl 63–612* (SBBG, RSA). Ventura Co., west of Reyes Pk., *Chandler 2049* (SBBG). An additional collection from the north slope of Reyes Pk. in Ventura Co. *(Wilken and Bekey 11875)* serves to document a chromosome count of $2n = 16$. In the San Rafael Mtns., *Collomia tinctoria* occurs at elevations from 1900 to 2200 meters on open gravelly slopes beneath the Yellow Pine Forest and flowers from late June to July.—Dieter H. Wilken, Department of Botany and Plant Pathology, Colorado State University, Fort Collins 80523.

An Asian Kelloggia (Rubiaceae)—Publication of *Kelloggia chinensis* Franchet [J. Bot. (Morot) 6:11. 1892] was duly noted in the Index Kewensis, but has been largely overlooked for eighty years. Most authors of floristic works covering portions of western United States have considered that *Kelloggia* is monotypic. Davis (*Flora of Idaho*. p. 648. 1952) says "One species in the genus". Munz (*A California flora*. p. 1045. 1959; *A flora of Southern California*. p. 770. 1974) says "One sp.". Ferris (*Illustrated flora of the Pacific States*· 4:24. 1960) says "A monotypic genus of western North America". Furthermore Willis (*A dictionary of the flowering plants and ferns*, ed. 6, p. 353. 1951), on whom we largely rely in such matters, says "1 W. N. Am.", and (ed. 7. p. 597. 1966) "1 SW U.S.". Exception must be made of Hitchcock et al. (*Vascular plants of the Pacific Northwest* 4:453. 1959), who mention that there are two species, *K. galioides* Torr. (Bot. Wilkes Exped. p. 332. t. 6. 1874) "and a similar one from Yunnan, China".

I have not seen the type (*Delavay 2588,* P) of *K. chinensis,* but there is in UC a specimen of another collection, a duplicate from P, that corresponds well with the original description. Neither date nor collector's name are given on the label, but the collection number is *2633* and the locality "Chine (Thibet or[ient]al: Tsekou". In a personal letter from J. C. Jolinon (Natural History Museum, Paris), who had

access to a sheet at P of the same collection, I am informed that the handwriting and the quality of the paper of the label both indicate that the specimen is probably Delavay's.

Corollas in the UC specimen of *Kelloggia chinensis* have considerably shorter tubes and relatively broader lobes than in *K. galioides,* the ovaries are shorter, and the anthers are much smaller. Franchet makes a point of the consistently pentamerous flowers of *K. chinensis,* but pentamerous flowers are also common in *K. galioides,* and it may well be that more abundant material would also show tetramerous flowers in *K. chinensis.* Stipules of *K. galioides* are usually entire or bifid, whereas those of *K. chinensis* are larger and fimbriate. Pedicels in our material of *K. chinensis* are much shorter, and the inflorescence therefore less lax, than in *K. galioides,* and there is no swelling of the pedicels just below the ovary, as is invariably the case in *K. galioides.*—LAURAMAY T. DEMPSTER, Jepson Herbarium, University of California, Berkeley 94720.

A flora of the Trinity Alps of northern California. By WILLIAM J. FERLATTE. 206 pp., figs., map. University of California Press, Berkeley. 1974. $10.95.

Northern California has few published local floras, those for Mts. Shasta and Lassen being exceptions. In the east the Warner Mts. are the meeting grounds at both high and low altitudes of Great Basin and Californian floras, and in the west the flora of the Pacific Northwest meets, dissolves into, or changes in contact with the Mediterranean-climate flora of California proper. In between all three floras mix. Whittaker has suggested (Madroño 16:5–23, 1961) that the Klamath Mts. area in general is a center of western diversity and persistence similar to the Cumberland Mts. of Kentucky in relation to the eastern hardwood forests.

Many exciting floristic finds have been made in this northwestern part of California recently. Ferlatte's book discusses the mountain flora above 1520 m (5000 ft) of a small but most interesting part, namely the high, eastern, mostly granitic part of the Trinity Alps. This is a glaciated mountain area with vegetation belts from alpine above some 2240 m (8000 ft) to 2743 m (9002 ft) on Thompson Pk., down through subalpine forest, red fir, and mixed conifer with montane chaparral as a probably non-zonal vegetation type.

In his area of less than ca 400 km^2 (170 mi^2) are 571 species, including 75 shortly discussed in an appendix, which is unfortunately so segregated. The book describes each taxon with indented and therefore short keys, morphological descriptions, vegetation zones in which the taxa are found, and localities with ecological notes, citations of specimens, and time of flowering. Illustrations include many fine plant drawings by Charles S. Papp that are lifelike and helpful plus eight pages of photographs, many of which are aerial views of the terrain. A few comments can be made. Recent "excursion floras" have incorporated innovations that have decreased their size and increased their usefulness. These improvements for field use deserve imitation. The book would have more room for a plant geographical analysis of the flora if species descriptions were shortened to the barest necessities, mainly for this purpose differentiating characteristics. The descriptions are well-written and perceptive, however, improving on Munz' or perhaps representing a smaller range of variation in specimens. A few synonyms might have been listed. Ecological descriptions could have been expanded since the author has had much experience in the area and access to herbarium collections.

Still, the format chosen is self-contained, and therefore the book is a fine guide to natural history for the many visitors who use the Salmon-Trinity Primitive Area. Reclassification to a Wilderness Area is pending, and the public land management agency involved, the U.S. Forest Service, has thus had presented to itself free an excellent basic inventory for a part of the area it must consider. Unfortunately, the

1972 proposal for reclassification suggested eliminating from wilderness status most of the presently reserved area of the Trinity Alps that Ferlatte studied. This is in spite of an annual almost 10 percent increase in recreational use over the last 5 years according to the Forest Service. The obvious answer to the current problem of too much use of wilderness, so much that use must be rationed, is to dedicate more lands to wilderness use from areas that are *de facto* wilderness. The Forest Service has allowed an ostensibly mining road into the heart of the area to persist, and entries under the 1872 Mining Law have been used to acquire title to public land. However, most commercial ore or placer deposits were mined out 30 years or more ago. Alternate sections in most of the proposed exclusion are owned by the Southern Pacific Railroad, and the Forest Service cannot acquire these lands without appropriations, which Congress and the executive branch have not made available. The obvious temporary solution is to classify as wilderness those sections (often in contiguous blocks of more than 5000 acres) that are federally owned and rely on local good sense plus zoning to see that privately owned lands are not "developed" in ways that destroy public values. One of these values is the flora that Ferlatte describes so well and handsomely.

This is an excellent, useful flora. We need more like it.—JACK MAJOR, Department of Botany, University of California, Davis 95616.

Washington wildflowers. By EARL J. LARRISON, GRACE W. PATRICK, WILLIAM H. BAKER, and JAMES A. YAICK. 376 pp., 64 color plates, 114 figs., 4 maps. Seattle Audubon Society, Seattle. 1974. $6.45.

Intended as a layman's guide to common Washington wildflowers this book includes 63 families and 1134 species. It was sponsored by 70 individuals and 12 organizations. It is notably free of typographical errors and is sturdily bound and conveniently sized for field use. Superficially, the guide is impressive, but beyond the colors and neat print an unfortunate disappointment exists.

Plants in figures 16, 20, 24, 27, 28, 33, and 63 are grossly misidentified; plate 19, identified as *Draba,* is a *Stellaria*. Figures 38 and 67 are printed upside down. Many b/w photos are of marginal quality, and some of people and general scenes contribute little to the guide's purpose. The authors stress wildflowers, but some photos of weedy species, instead of native, were used for illustrations.

To exclude weedy, shrubby, and less common species, as was the intent, a work must confront problems of definition. This was not done and arbitrariness is obvious. For example, the shrub *Potentilla fruticosa* is listed, whereas herbaceous *Rubus pedatus* and *R. pubescens* are not; *Lepidium perfoliatum* and other non-native plants are given, but common naturalized plants, e.g., *Conium maculatum, Nymphaea odorata* are not. *Pedicularis rainierensis,* a Mt. Rainier endemic appears, but *Tauschia stricklandii,* also a Rainier endemic, does not. Many common plants are also omitted, e.g., *Aster chilensis, Senecio pauperculus. Calypso bulbosa* is not "endangered", as stated.

The discrimination against common naturalized or weedy species will stump some users of the book. At least 35 common genera are excluded. The publication would be strengthened by the addition of some of those genera. As is, the guide user should avoid botanizing roadsides or disturbed areas. In general, the treatment appears stronger for west of the Cascades and less comprehensive for northeast and central Washington.

Arrangement of families is phylogenetic; however, genera and species appear in the order they artificially key out. This arrangement of genera and species is inconvenient and makes it difficult to locate taxa except by index. The guide would be easier to use if taxa had been listed alphabetically. Keys are stressed by the authors

as being simple to use: measurements are given in inches vice metric units; some terms are simplified; and fewer species are treated. Otherwise, key leads seem similar to those in Hitchcock and Cronquists' *Flora of the Pacific Northwest*. Absent are remarks about herbaria and their use in plant systematics; nor is there acknowledgment to regional works that make local guides possible.

Topical essays are located in the body of the keys, apparently to minimize technical reading burdens for laymen. Topics appear in random order and are not indexed. It may be diversionary and undemanding to stumble across the essays, but for interested persons it is a burden.

A discussion on plant habitats is general and loose. Specific features—dune, salt marsh, rain forest—are mentioned for western Washington, but for elsewhere the authors revert to geologic provinces and Merriam's life zones. Life zone maps were taken from C.V. Piper's *Flora of the State of Washington*, 1906. Franklin and Dryness' *Natural vegetation of Oregon and Washington* (USDA For. Ser. Tech. Rept. PNW-8, Portland, 1973) apparently was not consulted, but Daubenmires' *Forest vegetation of eastern Washington and northern Idaho* (Wash. Agr. Expt. Sta. Bull. 60, 1968) is mentioned.

Statements such as, "Technical manuals treating the flora of Washington are for the most part sparsely illustrated", strain credulity in view of two major illustrated floras for the area. Another, ". . . grouping by flower color is not feasible, as there are relatively few flower colors", overlooks Philip Munz' guides to California wildflowers, and Peterson and McKennys' *A field guide to wildflowers of northeastern and northcentral North America,* 1968.

Responsibilities for deficiencies in *Washington wildflowers* belong to the professionals who authored the book, not the well-intentioned sponsors or enthusiasts who encouraged the production. Unfortunately, an unsuspecting public may bear the cost.—Earle F. Layser, Nez Perce National Forest, Grangeville, Idaho 83530.

Profiles of California vegetation. By William B. Critchfield. 54 pp., 1 fig., 57 profiles. U.S.D.A. Forest Service Research Paper PSW-76. 1971. $2.50.

The distribution of forest trees in California. By James R. Griffin and William B. Critchfield. 114 pp., 3 figs., 84 maps. U.S.D.A. Forest Service Research Paper PSW-82. 1972. $1.75. Both available from Superintendent of Documents, U.S. Government Printing Office, Washington, D.C. 20402.

These two volumes are contemporary compilations based largely on results of the California Vegetation Type Map Survey (VTM) conducted by the U.S. Forest Service some 35 years ago. The history of this ambitious project, which involved field mapping of dominant vegetation and extensive documentation with herbarium specimens, is briefly described in each publication. Both are of great potential usefulness to those engaged in ecological studies in the forested portions of California and the Lake Tahoe-Sierran corner of Nevada, which also came under jurisdiction of the VTM survey. These publications are avowedly of limited or no usefulness in the transmontane deserts of the south and the Great Basin intrusions of the north of California. With these exceptions, the two volumes, together with the original published vegetation type maps (see Madroño 22:153), provide a very good picture of forest and other vegetation in much of California in the 1930's. It is hardly surprising that vast changes have occurred in California's vegetation in the four intervening decades, but it is very lucky for those investigating these changes that such thorough evidence from the past is available for comparison.

The bulk of the first publication is devoted to 57 elevational profiles with vegetation symbols, representing north-south or east-west transects of quadrangles surveyed by VTM teams. They were drafted by M. N. Dobrotin to accompany maps of

these quadrangles as published. Of the profiles reproduced here, only fourteen actually accompanied maps, so the majority were previously unpublished. The great length of the profiles (about 23–63 km long at 0.77–1.3 km per cm) is accommodated by a folded page format that reduces shelf dimensions to a manageable 26 × 20 cm. The VTM survey used 15-minute and 30-minute topographic quadrangles as their base maps and numbered these in a common sequence from north to south, but profiles of the two groups are separated in this publication. The dual numerical sequence thus created is confusing to some users but is perhaps justifiable considering the difference of scale between the series. Critchfield has enhanced the value of the profiles by providing interpretive tables for the pictographic and alphabetic vegetation symbols appearing in them and by compiling a table of dominant species represented, with their occurrence. One can only be sorry that the excellent detail of the original pictorial symbols has been obscured in the necessary reduction to book size, but their intent is plain enough. All told, these profiles are an admirable representation of vegetation in relation to geographical and topographical features and present a three-dimensional view of California's vegetation that is hard to find elsewhere.

Maps and descriptions of natural distributions of 86 tree species in California and the VTM portion of Nevada comprise the second publication. Though also largely based on data of the VTM survey and its successor, the California Soil-Vegetation Survey, the authors have compiled their maps and descriptions from a much wider range of sources, as their bibliography of some 250 items attests. The maps show detailed, documented distributions that indicate gaps in our knowledge as clearly as known localities. These are a far cry from the overly generalized, poorly drafted maps compiled for volume 1 (1971) of E. L. Little's *Atlas of United States trees* and hark back instead, to the meticulous maps prepared under the direction of George B. Sudworth (1861–1927) to accompany his bulletins on Rocky Mountain trees. Similarly, the verbal descriptions, which discuss elevational, taxonomic, and ecological matters, are reminiscent of Sudworth's painstaking distributional observations in *Forest trees of the Pacific Slope* (1908), though they plainly show the expansion of knowledge since then, and the references show that accuracy in delimiting distribution can no longer be the result of field experience by one man. While being very favorably impressed by the care the authors have taken in assembling this very valuable compilation (they worked with the printers for over a year before they were satisfied with the printed quality of the maps), inevitable errors have crept in. *Plantanus racemosa* is a simple typographical error, but most of the localities shown for *Populus angustifolia* are probably based upon misidentifications. There are some places for differences of opinion. *Castanopsis chrysophylla* should probably be transferred to *Chrysolepis* Hjelmqvist (1948, cited in their bibliography). One questions the omission of tree willows, for they are often quite important in riparian vegetation, and, while VTM crews ignored them in mapping, their specimens are readily accessible in UC. Blind acceptance of C. B. Wolf's splinter species of *Cupressus* (Aliso 1:1–250, 1948) seems unwarranted but, pending critical evaluation, is perhaps preferable to E. L. Little's irrational groupings (Phytologia 20:429–445, 1970). Personal preferences aside, Griffin and Critchfield have done a fine job, and these two paperbound volumes can well serve the general public and environmental interest groups, as well as botanists and foresters.—James E. Eckenwalder, Department of Botany, University of California, Berkeley 94720.

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APACHERIA CHIRICAHUENSIS: A NEW GENUS AND SPECIES FROM ARIZONA

CHARLES T. MASON, JR.
Herbarium, College of Agriculture
University of Arizona, Tucson 85721

To find a new species in Arizona is unusual, but to find an undescribed genus is indeed rare, especially when the discovery is made in the well botanized Chiricahua Mountains of southeastern Arizona.

Apacheria C. T. Mason, gen. nov. Frutex parvus. Folia opposita parva integra vel triloba; stipulae minutae. Flores singulares sessiles vel brevipedunculati; hypanthium praesens. Sepala 4. Petala 4. Stamina 8. Carpella 1 ad 4 plerumque 4 libera; ovula 2. Fructus folliculares. TYPUS: *A. chiricahuensis* C. T. Mason.

Apacheria chiricahuensis C. T. Mason, sp. nov. Frutex ad 50 cm altus. Folia oblanceolata vel spathulata 3.5–7.5 mm longa 1.0–2.3 mm lata apiculata glabra. Sepala 3.0–3.5 mm longa. Petala alba 4–5 mm longa. Stamina labris hypanthiorum insidens; antherae 0.5–1.0 mm longae; fila 3 mm longa. Ovaria hispidula. Stigmata linearia introrsa. Folliculi prominenter venosi. Semina 1 vel 2 minutissime papillose brunnea reniformia 1.5 mm longa 1.0 mm lata; endosperma abunda. Fig. 1.

TYPE: Arizona, Cochise Co., crevices in rock outcrops and ledges, West Picket Park Research Natural Area, Chiricahua National Monument, ca 5,800 feet in Upper Picket Canyon, mid-May 1973, *William Moir s.n.* (Holotype: ARIZ; isotypes to be distributed.)

In addition to the type material, a specimen collected in Picket Park by O. M. Clark *(8950)* was examined at the Chiricahua National Monument Herbarium. Further collections were made by the author from Picket Canyon *(Mason 3138, 3139)*, from adjacent Bonita Canyon *(Mason 3137)*, and from Echo Canyon Trail *(Mason 3145)*. Since attention has been directed to this new genus, a specimen collected by Chris Barry *(s.n.)* from Surprise Canyon has been examined, and Dr. Vince Roth of the Southwest Research Station has reported finding specimens of it in the Heart of Rocks Area (pers. comm.). All localities are in Chiricahua National Monument. So far *Apacheria chiricahuensis* has been observed growing only in crevices and on ledges of bare north and south exposed rhyolitic rock outcrops.

This endemic small shrub is named to honor the Chiricahua Apache Indians who once inhabited the area.

The new taxon is assigned as the second genus in the family Crossosomataceae although it also shows affinities to members of the Saxifragaceae and Rosaceae. It is similar to *Crossosoma bigelovii* Wats. in its

MADROÑO, Vol. 23, No. 3, pp. 105–168. July 1, 1975.

glabrous, highly branched habit and rock crevice habitat. The white flowers of each are borne singly on the ends of short shoots and have a similar perigynous cup with the perianth parts and stamens arising from the rim of the hypanthium. In the base of the concave axis are the free

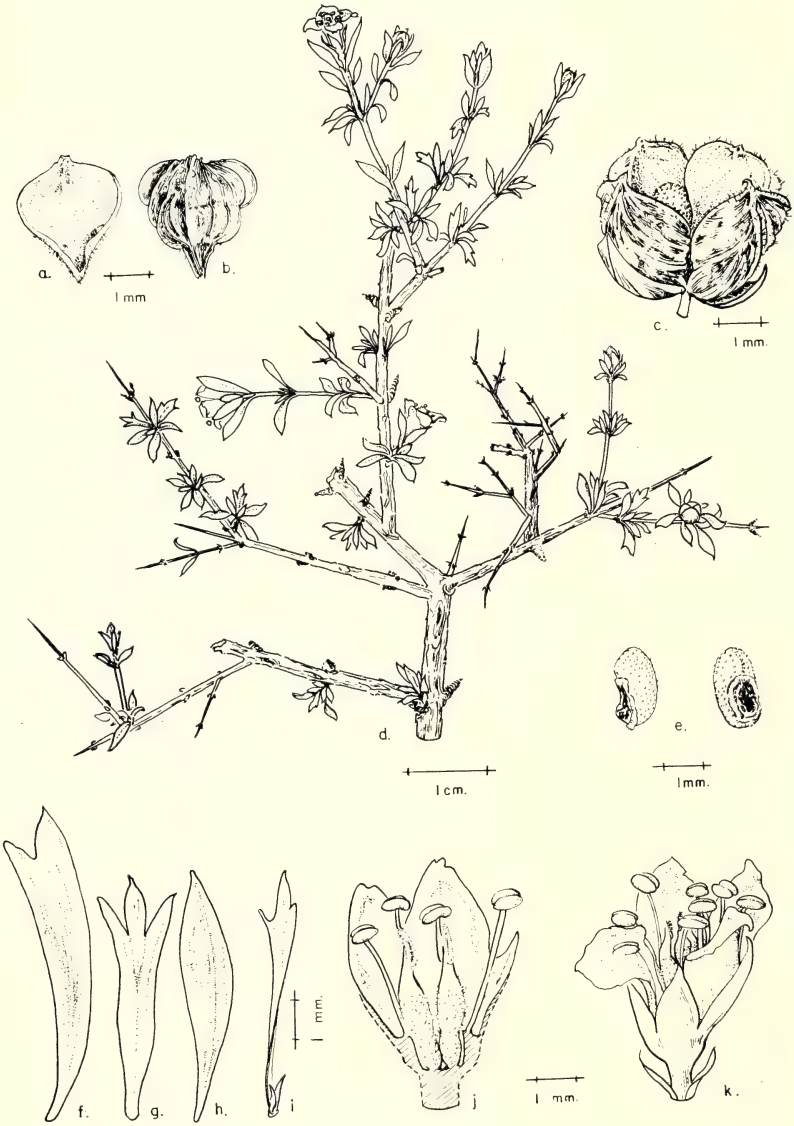

FIG. 1. *Apacheria chiricahuensis* C. T. Mason. a and b, single open follicle (a, adaxial, b, abaxial); c, four follicles in situ; d, branch; e, seeds; f, g, and h, leaf variation; i, leaf with stipules; j. flower (median longitudinal section); k, flower (entire). Illustrations by Patricia Mason.

carpels, which mature into follicles. The seeds of both tend to be reniform and possess an aril. The straight or slightly curved embryos are embedded in the endosperm. The pollen of *Apacheria* is not significantly different from that of *Crossosoma bigelovii* (fig. 2). *Apacheria* pollen is spherical with an average size of 14.8 μm from pole to pole and 15.2 μm in equatorial diameter. The exine is semitectate and per-reticulate with a heterobrochate reticulum. The grains are tricolporate; the elongate colpi are rounded at the ends. The pores are rounded, 4 μm in diameter and partially hidden beneath the exine at the equator. *Crossosoma bigelovii* pollen differs only on a slightly larger size (18.7 μm polar diameter; 20.0 μm equatorial diameter) and larger pores (6 μm diameter). However, the variability in each of these quantities is as great among pollen grains of the same species as between pollen grains of the two different species.

Crossosoma bigelovii differs from *Apacheria* in having alternate, estipulate leaves and 5-merous flowers with 20 or more stamens. The carpels of both genera are similar in shape, but those of *Crossosoma* contain numerous ovules. The aril is large and fimbrillate in *Crossosoma* but entire to fimbriolate in *Apacheria*.

The Philadelphieae, (Saxifragaceae, subfamily Hydrangeoideae) has also been considered as a possible placement for this new taxon on the basis of the opposite leaves, tetramerous flowers, and seeds with endosperm. Comparisons between *Apacheria* and some native woody species of Saxifragaceae in southeastern Arizona, such as *Jamesia, Philadelphus, Fendlerella*, and especially *Fendlera*, show some similarities in vegetative

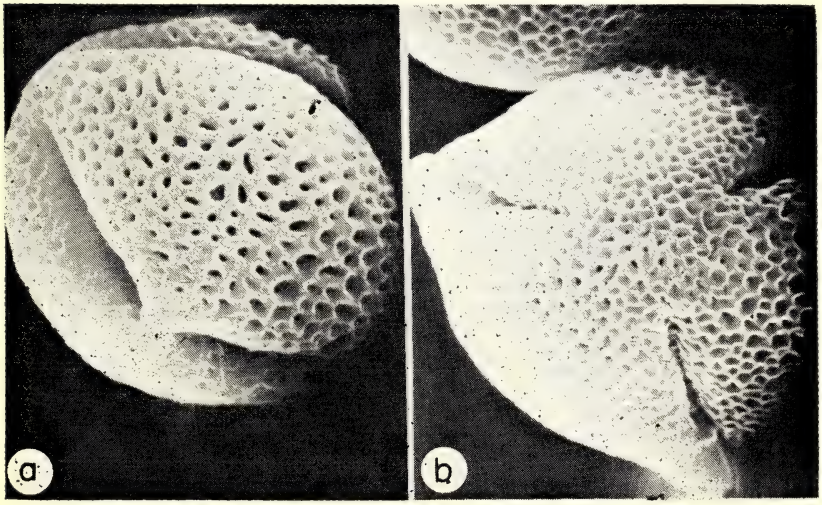

FIG. 2. Scanning electron photomicrographs of pollen: a, *Apacheria chiricahuensis;* b, *Crossosoma bigelovii.*

and floral morphology, but *Apacheria* differs in having stipules, an aril on the seeds, and wholly superior follicular fruits (rather than capsules) developing in a perigynous cup. Furthermore, this new species is glabrous except for the hispidulous ovaries, whereas species of the other genera are most commonly pubescent and often copiously so.

The Spiraeoideae (Rosaceae) was also considered because of the follicular fruits in a concave receptacle but was ruled out on the basis of the endosperm and aril of the seeds and the opposite leaves. *Lyonothamnus,* the only southwestern genus in the Spiraeoideae with opposite leaves, shows a similarity only in the follicular fruits. The resemblance to *Coleogyne,* a genus of southwestern United States in the subfamily Rosoideae, is restricted to the opposite leaves.

The pollen of several potentially related species in the Saxifragaceae and Rosaceae was studied for a comparison with *Apacheria.* In no case was the similarity as close as that of *Crossosoma.*

I express my appreciation to and acknowledge the assistance of Dr. Allen Solomon, Department of Geosciences, University of Arizona, in comparing and describing the pollen of *Apacheria, Crossosoma,* and other genera.

A NEW SPECIES OF GALIUM (RUBIACEAE) FROM THE SIERRA MADRE ORIENTAL

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On 18 June 1948, F. G. Meyer and D. J. Rogers collected a very distinct and in several ways remarkable *Galium* in the Sierra Madre Oriental of Mexico. Although the general appearance of the plant immediately sets it apart from any other Galium that I have seen, its most remarkable character proves to be the long-campanulate or tubular corolla. Of several *Galium* taxa in southwestern United States and northern Mexico that have campanulate corollas, including most notably *G. hilendiae* ssp. *kingstonense* (Demp.) Demp. & Ehrend., *G. pringlei* Greenm., *G. correllii* Demp., *G. mexicanum* H.B.K., *G. pendulum* Greenm., and *G. carmenicola* Demp., the new species has the longest corollas (fig. 1 A). The next longest are those of *G. hilendiae* ssp. *kingstonense,* a member of a quite different species group, and *G. pringlei* (fig. 1 E), which occurs a little farther north in the same mountain range as the new taxon. Indeed the difference in size, shape, and posture, even between the two corollas illus-

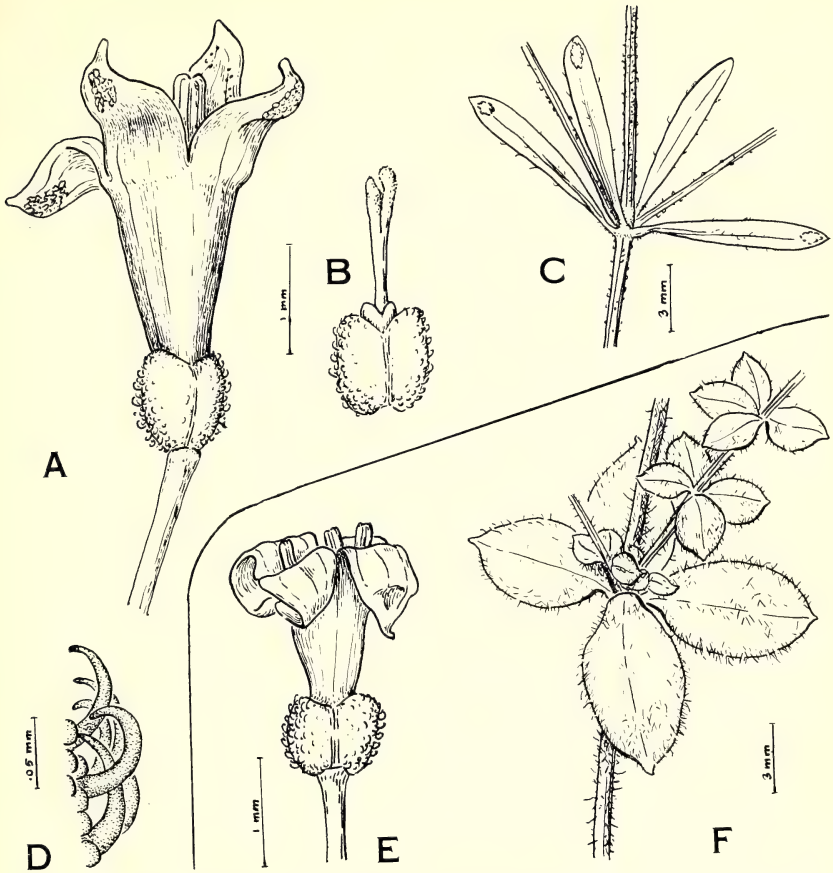

Fig. 1. Leaves, flowers, and details of *Galium lacrimiforme* and *G. pringlei*. A–D, *G. lacrimiforme:* A, flower, with one stamen showing; B, gynoecium; C, node, showing leaves and branches; D, hairs from ovary. E–F, *G. pringlei:* E, flower; F, node, showing contrast between primary and secondary leaves.

trated, is not so great as to be incompatible with their coming from conspecific plants. In other respects also, the flowers are alike, namely in their strongly arcuate, apically-directed ovary hairs (fig. 1 D), their oblong, little-exserted anthers, and their linear, rather than globular, stigmas (fig. 1 B). Vegetatively, however, these plants are so strikingly different that there can be no doubt of their being specifically separate. *Galium pringlei* has mostly elliptical to orbicular leaves (fig. 1 F), and the stems and leaves are more or less densely covered with long spreading hairs, whereas the new species has linear to oblanceolate leaves (fig. 1 C), and the indumentum is altogether different, the stems having very short curly hairs and the leaves a very few short apically directed hairs. Habit also appears to be quite different in the two species, but caution

should be observed on this point, inasmuch as there is only one collection of the new species, although we have 12 collections of *G. pringlei*. An outstanding characteristic of *G. pringlei* (fig. 1 F) is that the secondary growth arising at the nodes of the long primary stems is conspicuously different, particularly in congestion and size of leaves, from the primary stems and leaves. In the type of the new species the plants are lower, and there is no obvious difference between primary and secondary stems and leaves. Although we cannot be sure that these differences in habit are valid, the difference in shape of leaves and in indumentum will, in my opinion, not be bridged.

The new species is named *Galium lacrimiforme* because of the elongated tear-drop shape of the leaves.

Galium lacrimiforme Dempster, sp. nov. Planta perennis herbacea; caules pilis crispis mollibus obtecti; folia quatuor uninervia, anguste oblanceolata, 4–12 mm longa, basin versus sensim angustata, apice rotunda vel leviter acuta, pilis paucis brevibus instructa; flores pauci perfecti, corollis glabris campanulatis, lobis quatuor patentibus, antheris oblongis vix exsertis, stigmatibus linearibus inclusis, ovario pilis sursum arcuatis obtecto; fructus maturi non visi.

Type: Nuevo Leon, 8 miles east of Dulces Nombres, 24° N., 99° 35′ W., *Meyer and Rogers 2586* (holotype, MO!; isotypes, GH! BM!). In oak-pine forest, at 1550 m.

Herbaceous perennial, rooting at the nodes; stems softly pubescent with downward-curling hairs; leaves 1-nerved, ascending, 4 to a node, 4–12 mm long, linear to oblanceolate, tapered gradually to a petiole, round or somewhat acute at apex, unarmed, the surfaces glabrous or with a few soft hairs; glandular cells clustered below the apices; flowers few, perfect, 2–3 mm long, apparently solitary in the axils or paniculately disposed in irregularly developed cymules on leafy branchlets, the true pedicels shorter than the flowers to nearly obsolete; corollas glabrous, narrowly campanulate, cleft about two-fifths, the 4 lobes spreading, blunt, punctate within, externally set with a cluster of glandular cells; anthers partly exserted from the corolla tube, about half as long as the tube; stigmas well included, linear, on style about as long as stigmas; fruit dry, of 2 hemispherical mericarps, set with short strongly arcuate or uncinate hairs; mature fruit not seen.

I thank Rimo Bacigalupi for editing the Latin.

Editorship of Madroño.—Terms of current editors of Madroño end December 1976. Successor(s) will be appointed no later than July 1976. Applications or recommendations for the Editorship are encouraged. They should be sent by October 1975 to L. R. Heckard, Madroño Editorial Search Committee, Botany—Jepson Herbarium, University of California, Berkeley, California 94720.

HYMENOCLEA PLATYSPINA (ASTERACEAE: AMBROSIEAE), A NEW SPECIES FROM BAJA CALIFORNIA

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Examination of plants sampled from two populations *(FS82* and *FS83)* separated by 8 km along Mexico Hwy. 5 in Baja California revealed a new taxon possessing some affinity with the *Hymenoclea salsola* complex (Peterson and Payne, 1973). All plants observed in the two localities were restricted to dry arroyos at the base of bajadas that extended several kilometers from the Sierra Pinta Mtns. The species shares with *H. salsola* the characteristics of spring flowering and the emergence of the involucral wings in several series from the surface of the pistillate head. The latter character is variable in *H. salsola* but contrasts with the uniform arrangement typical of *H. monogyra* wherein the wings are arranged in a single whorl at the center of the involucre. *Hymenoclea platyspina* can be distinguished from *H. salsola* by the characters listed in Table 1. The most important difference is reflected by the specific epithet, emphasizing the presence of a flattened spine that emerges from the end of the thickened midrib of the pistillate involucral wing.

Hymenoclea platyspina Seaman, sp. nov. Frutex ad 15 dm altus cortice flavoviridi stramineave. Rami graciles ascendentes. Folia sessilia velutina 1–4 cm longa bipinnatifida tripinnatifidave lobis filiformibus epidermide globulis resinosis pellucidis numerosis. Capitula staminata pistillataque intermixta axillaria. Involucrum staminatum late cupuliforme lobulis 5–6 ovatis vel deltoideis 3–4 mm latis tomentulosis epidermide globulis resinosis pellucidis numerosis; flores 6–9 rare paucores; receptaculi paleae corollis breviores lineares margine villosae apicibus spathulatis ad maturitatum nervo medi spiniformi; corollae infundibuliformes glabrae; antherae apice acutae; stylus rudimenti staminibus brevioris parte stigmatica penicillata. Involucrum pistillatum ca 6 mm altum fusiforme rostratum phyllariis 14–18 cartillaginis dorsiventraliter complanatis apice spiniformibus lateraliter alatis alis oblanceolatis ad basin concavis aliquando foveatis; flos solitarius centralis omnino inclusis. Fig. 1.

Type: Baja California, 101.6 km N of San Felipe, 31°48′N, 115°7′W, on Mexico Hwy. 5, growing in a dry arroyo on soil derived from a basalt-like igneous rock, 3 Apr 1972, *F. Seaman and R. Hartman FS-82(3),* (Holotype, TEX; Isotypes distributed to UC, MEXU). Known only from the type locality where it grows along an 8 km stretch of the highway.

Acknowledgments

I thank Dr. M. C. Johnston for the Latin translation and Dr. B. L. Turner for assistance in preparing the description. Financial support of the National Science Foundation (Grant GB29576X and GB3604) is also appreciated.

TABLE 1. DIAGNOSTIC CHARACTERS SEPARATING HYMENOCLEA PLATYSPINA FROM THE H. SALSOLA COMPLEX (Peterson and Payne, 1973; 1974).

Character:	*H. salsola* var. *pentalepis*	*H. salsola* var. *salsola*	*H. salsola* var. *patula*	*H. platyspina*
Involucre				
wing morphology	hyaline without terminal spines	hyaline without terminal spines	hyaline without terminal spines	thickened midrib, terminated by spine
wing length (mm)	3.20±0.82	3.79±0.37	4.51±1.01	3.20±0.41
wing width (mm)	3.59±1.07	4.50±0.94	5.38±0.98	1.4±0.37
length/width	0.89	0.84	0.82	2.3
wing arrangement	whorled near center of involucre body; emergent from involucral body	spirally arranged or in several series; emergent from involucral body	spirally arranged or in several series; appressed to involucral body	spirally arranged or in several series; emergent from involucral body
number of wings	7.00±1.77	9.70±1.82	13.20±1.98	15.01±1.20
Receptacular paleae in the staminate head	without thickened midrib and terminal spine	without thickened midrib and terminal spine	without thickened midrib and terminal spine	with thickened midrib and terminal spine
Leaf morphology	filiform, the lower pinnately few lobed	filiform, the lower pinnately few lobed	filiform, the lower pinnately few lobed	pinnately divided throughout plant, with large filiform segments

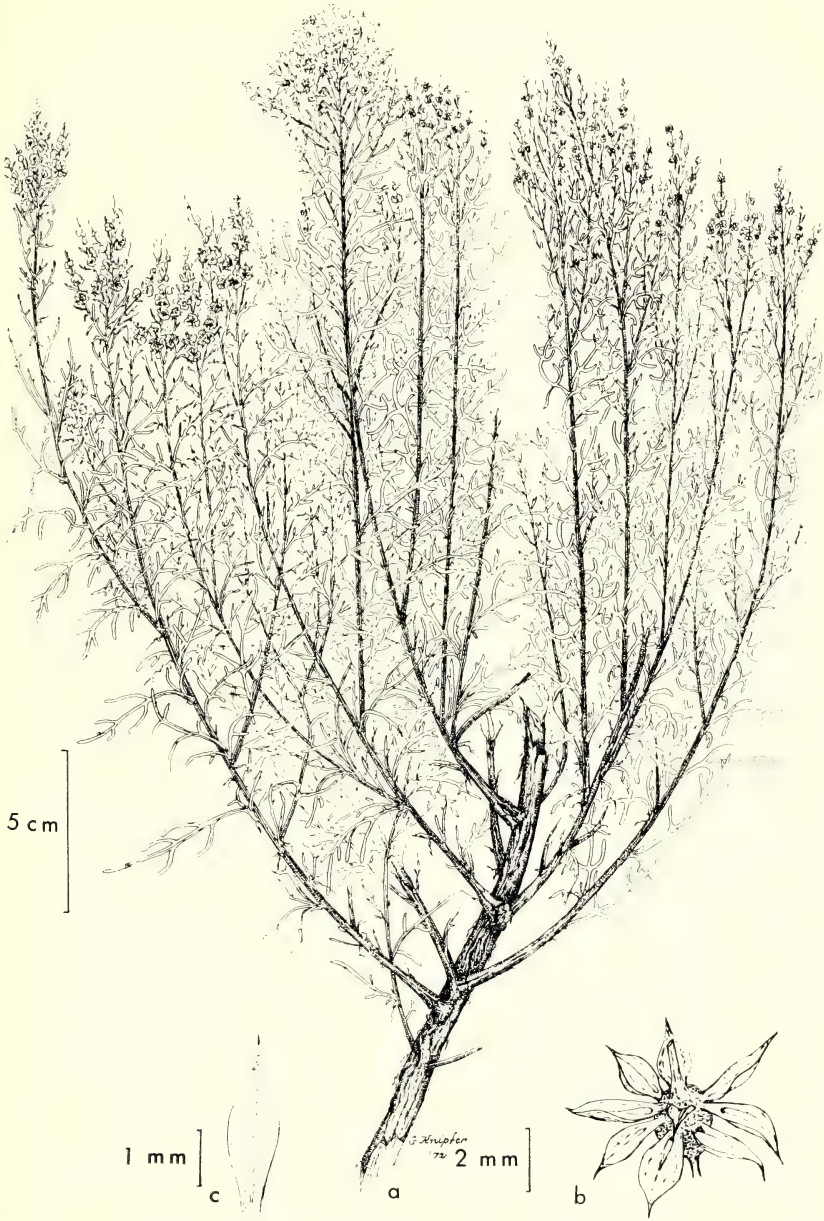

FIG. 1. Habit and morphological details of *Hymenoclea platyspina;* A, vegetative portion with immature pistillate heads; B, a mature pistillate head; C, an involucral wing.

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EFFECTS OF POWER TRANSMISSION LINES ON VEGETATION OF THE MOJAVE DESERT

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The natural vegetation of the Mojave Desert has been subjected to a variety of manmade disturbances including construction activity, agricultural clearing, recreational traffic, military maneuvers and testing, mining, and many more. Disturbance activities have a primary impact at their onset and sometimes a secondary impact if disturbance continues. An assessment of disturbance to vegetation involves estimating both the area disturbed and the species affected, along with evaluating the course and rate of recovery. In cases compounded by continued disturbance, many secondary effects may develop that may cause drastic changes in the distribution of organisms and in organism interactions.

There are a few reports discussing the impact that various disturbances have had on the Mojave Desert vegetation. Beatley (1965, 1966) and Wallace and Romney (1972) discussed the effect of short-term disturbance on the vegetation of nuclear test sites in southern Nevada. Vasek et al. (1975) described the effect of pipeline construction in the Lucerne Valley region of California, and called attention to the extreme ages of some creosote bushes *(Larrea tridentata)*. Wells (1961) described a successional pattern following the cessation of continued disturbance on the streets of a Nevada ghost town, and Davidson and Fox (1974) evaluated the effects of intermittent off-road motorcycle activity. However, to our knowledge, no evaluations are available on the disturbance to vegetation by powerline construction.

The construction of power transmission lines involves clearing access roads, constructing pylons, and stringing cables and wires between pylons. Disturbance ceases after construction is complete, except for continued use of access roads by maintenance patrols. In essence, then, power line construction involves devegetation on access roadways, temporary destruction of vegetation under the power pylons, and temporary

disturbance of vegetation between pylons by trampling. Our report attempts to estimate the impact of power transmission line construction and maintenance on the vegetation of the Lucerne Valley region of the Mojave Desert. The investigation was supported by the Southern California Edison Company as part of an environmental impact study associated with their proposal for a new electric generating plant in the Lucerne Valley region of San Bernardino County, California.

Methods

We selected two existing Southern California Edison power transmission lines in the Lucerne Valley region for study: the North Lugo to Pisgah 220 KV transmission line constructed in 1937, and the older of the twin lugo to Eldorado 550 KV transmission lines completed in 1970 and 1971 (fig. 1). Our method was to sample vegetation on and near the right of way at each of six study areas along the 1937 transmission line and five study areas along the 1970 transmission line. Physical characteristics of the study areas are listed in Table 1. Each study

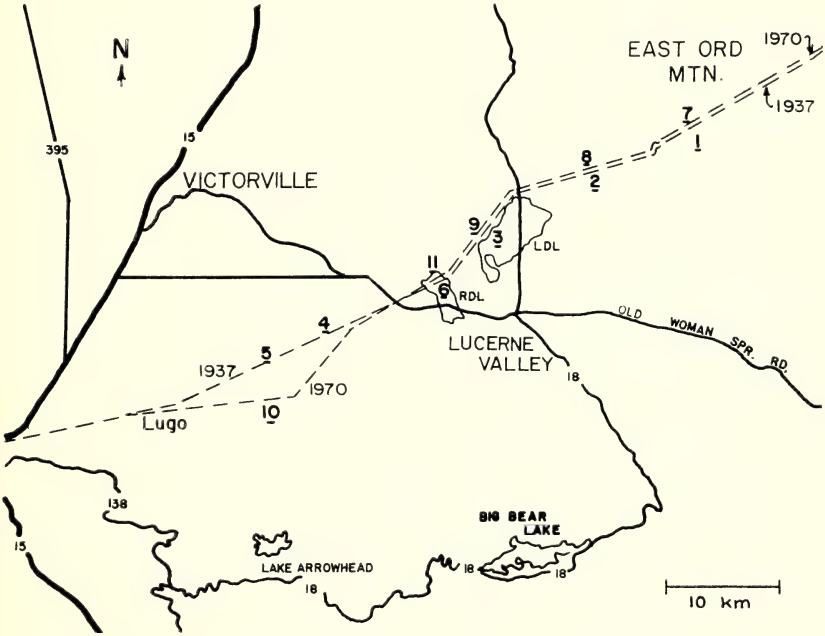

Fig. 1. The greater Lucerne Valley region (San Bernardino Co.) of Southern California showing the paths of power lines studied and the location of the areas sampled. The dashed line with study area sequence 5, 4, 6, 3, 2, and 1 represents the powerline constructed in 1937. The dashed line with study area sequence 10, 11, 9, 8, and 7 represents the power lines constructed in 1970–71. Local highway numbers and other landmarks are indicated. RDL = Rabbit Dry Lake; LDL = Lucerne Dry Lake.

TABLE 1. PHYSICAL CHARACTERISTICS OF STUDY AREAS.

Study areas	Power line	Topographic location	Exposure slope	Surface stability	Substrate origin	Substrate composition	Surface heterogeneity	Elevation (meters)
1, 7	Both	Rocky wash	South, gentle	Active erosion	Flood alluvium	Rocky to sandy	High	1036
2, 8	Both	Fan	Gentle	Stable	Alluvium	Sandy gravel	Low	940
3, 9	Both	Near dry lake	Level	Stable	Alluvium	Silt to sand	Moderate	883
4	Old	Valley bottom	Level	Stable	Alluvium	Sandy gravel	Low	990
5	Old	Valley bottom	Level	Stable	Alluvium	Sandy gravel	Low	960
10	New	Fan	North, moderate	Stable	Alluvium	Sandy gravel	Low	1100
6, 11	Both	Edge of dry lake	Level	Stable	Alluvium	Silt	Low	900

area was considered a separate experiment, the total representing a spectrum of disturbances. At each study area we sampled four belt transects, 100 m long and 2 m wide. The four transects were established as follows: transect A, a control transect at least 50 m away from the power line in undisturbed vegetation; transect B, midway between two pylons and directly under the central transmission wire; transect C, at the edge of the access road; and transect D, directly under the pylons. Since the pylons do not constitute a linear belt area, data from several consecutive pylons were pooled until a 200 m^2 area equal to each belt transect was sampled. Therefore, the area under four different pylons on the old powerline or the area under two consecutive pylons on the new powerline was included as one transect. The two selected powerlines provide a 33-year comparison reference frame and enable a reasonable estimate of vegetation recovery time for this type of disturbance.

Our observations are restricted to shrubs and suffrutescent perennials because samples were taken in mid-summer when herbaceous perennials and annuals were essentially absent. Therefore, in this paper ground cover refers to perennial ground cover by shrubs and suffrutescent perennials. The diameter of each shrub or suffrutescent perennial was measured directly in centimeters. Assuming that, on the average, plants cover a circular ground area, the ground cover for each plant was calculated from its radius and summed for each species in each transect. Our primary information, therefore, consists of plant density, ground cover, and species composition for each transect. In our analysis of the data, each perennial species is classified in one of two functional groups, long-lived or short-lived (Vasek et al., 1975), as determined from the literature (Muller, 1953; Muller and Muller, 1956) and our judgment. Percent ground cover of each functional group and of several important constituent species is calculated for each transect. Transects are then compared by a Community Quality Index (CQI) based on total perennial ground cover and the proportion of ground cover occupied by long-lived species (Vasek et al., 1975). The Community Quality Index (CQI) takes into account a measure of site productivity and an estimate of relative community age, thus providing an objective estimate of the ecological value (Suffling et al., 1974) of a vegetation. We judge dense vegetation of mature long-lived plants to be more valuable and have higher quality (COI) than sparse vegetation of quick growing pioneers (low CQI).

For purposes of general comparison, we observed ten other transects representing undisturbed vegetation south and west of East Ord Mountain (fig. 1).

Results

Regional Vegetation

Predominant vegetation in the Lucerne Valley region belongs to the creosote bush scrub community (community nomenclature of Munz and Keck, 1949). It occurs generally on slopes, alluvial fans, valley flats,

washes, and on low mountains. In alkaline seeps and valley bottoms the creosote bush scrub community is often replaced by a salt bush scrub community (a departure from Munz's community nomenclature due to our preference for naming plant communities and vegetation after plants rather than topographic features) presumably because of the high salt content of the soil. At higher elevations it is replaced by either pinyon-juniper or joshua tree woodlands, probably in response to more favorable rainfall and moisture conditions.

In the Lucerne Valley region, creosote bush scrub vegetation is highly variable. Its composition in terms of relative vegetation cover ranges from about 19 to 98 percent *Larrea tridentata* (species nomenclature follows Munz, 1974) as shown in ten representative transects from the region south and west of East Ord Mountain (Table 2). The total perennial ground cover of these ten reference transects ranges from about 7 to 27 percent. The number of perennial plants ranges from 7 to 45 per 100 m^2 and these include from 3 to 12 species. Similar variation was observed by Beatley (1974) in the Mojave Desert of southern Nevada where perennial ground cover ranged from 7 to 23 percent for 23 plots in creosote bush communities and, of that cover, 9 to 85 percent was provided by *Larrea*. Variation in average plant density from 1 to 100 per 93 m^2 plot was reported by Woodell et al. (1969) for eight scattered Mojave Desert localities.

The amount of ground cover provided by *Ambrosia dumosa,* a common associate of *Larrea*, ranges from 0 to 18.3 percent (Table 2). Long-lived species, including *Larrea* and *Ambrosia,* contribute about 60 to 100 percent of the total perennial plant cover. Other long-lived species (observed on the ten reference transects) that form a significant fraction of the ground cover on at least one of the reference transects belong to such genera as *Krameria, Lycium, Cassia, Ephedra, Opuntia,* and *Atriplex* (Table 3). The major short-lived species (in terms of density and ground cover) is *Hymenoclea salsola.* Other short-lived species listed in Table 3 constitute less than 1 percent of the total cover. The plant cover provided by short-lived species on the ten reference transects ranges from 0 to about 34 percent, mostly provided by *Hymenoclea.* Variation among these ten transects is quite apparent and can be partly explained by habitat differences (Table 2). The general characteristics of each transect can be summarized in one number, the Community Quality Index. Indices, ranging from 24 to 50 (Table 2), are rather high as compared to CQI's for creosote bush scrub communities in the mountainous region to the north. Vasek et al. (1975) found COI ratings up to 44 in the Lucerne Valley region but north of the Ord Mountains ratings ranged from 15 to 28.

Vegetation Along Power Lines

The powerlines in the Mojave Desert region under study mostly traverse creosote bush scrub vegetation (study areas 1–5 and 7–9). How-

TABLE 2. ANALYSIS OF REGIONAL VEGETATION BASED ON 10 REFERENCE TRANSECTS SOUTH AND WEST OF EAST ORD MOUNTAIN. TR = transect sample number; GC = ground cover; Density = number of individual plants; LL = long-lived species; SL = short-lived species; CQI = Community Quality Index.

TR	Total perennial GC%	Density per 100 m²	Number of species	Relative plant cover (% of total)						CQI	Site
				Larrea	*Ambrosia*	Other LL	All LL	All SL	*Hymen-oclea*		
31	10.69	11.5	5	36.67	0.00	36.20	72.87	27.13	27.13	27.91	Rocky wash
33	16.32	25.5	5	54.42	0.00	22.49	76.91	23.09	20.98	34.10	Rocky wash
43	10.74	21.0	5	89.29	2.79	7.49	99.53	0.47	0.00	32.69	Rocky alluvial slope
45	6.96	22.5	3	89.08	10.63	0.00	99.71	0.29	0.00	26.34	Silty wash
44	12.94	7.0	3	97.91	0.15	1.93	100.00	0.00	0.00	35.97	Sandy bajada
46	18.87	43.5	5	63.36	18.27	11.23	92.86	7.14	7.14	42.06	Sandy bajada
48	27.48	45.0	12	55.06	0.18	23.51	78.75	21.25	20.82	46.52	Gravelly wash
47	9.86	26.0	10	19.37	1.42	38.95	59.74	40.26	34.38	24.27	Gravelly wash
52	16.04	26.5	8	37.97	7.17	46.57	91.71	8.29	8.23	38.35	Silty wash
53	26.07	27.5	6	54.09	5.18	39.85	99.12	0.88	0.35	50.83	Silty wash

TABLE 3. PERENNIAL PLANT SPECIES CLASSIFIED BY RELATIVE AGE SPAN AND LISTED IN ORDER OF DECREASING TOTAL GROUND COVER FOR THE TEN REFERENCE TRANSECTS. (See Table 2; combined area = 2,000 m^2.) LL = long-lived perennial; SL = short-lived perennial; (?) = some uncertainty regarding age span.

SPECIES	Total coverage (m^2)	Relative age
Larrea tridentata	179.86	LL
Hymenoclea salsola	35.94	SL
Atriplex polycarpa	21.28	LL
Ambrosia dumosa	15.98	LL
Lycium cooperi	10.76	LL
Lycium andersonii	10.24	LL
Atriplex canescens	5.72	LL
Krameria parvifolia	5.58	LL
Opuntia ramosissima	4.96	LL
Cassia armata	2.40	LL
Salazaria mexicana	3.92	(?)
Ephedra californica	3.70	LL
Yucca schidigera	3.06	LL
Acacia greggii	2.26	LL
Encelia farinosa	1.20	LL
Stephanomeria pauciflora	0.88	SL
Thamnosma montana	0.78	LL
Sphaeralcea ambigua	0.42	SL
Chrysothamnus paniculatus	0.40	LL
Eriogonum inflatum	0.30	SL
Echinocereus engelmannii	0.08	LL
Opuntia basilaris	0.08	LL
Opuntia echinocarpa	0.04	LL
Haplopappus cooperi	0.04	SL
Machaeranthera tortifolia	0.02	SL
Fagonia californica	0.02	SL

ever, in the bottom of Lucerne Valley (study areas 6 and 11) they cross two dry lakes in alkali sinks with salt bush scrub vegetation, and west of Lucerne Valley (study area 10) they traverse various scrub woodland communities dominated by Joshua Trees *(Yucca brevifolia)* or California Junipers *(Juniperus californica)*. Data for the salt bush scrub (areas 6 and 11) are presented separately (Table 6) because the habitat and the plant community on the dry lake differ considerably from the creosote bush scrub community and its habitats and because a complete set of four transects for each powerline was not obtained. The road edge transects and a transect under the wire were located on the dry lake playa and consequently had no plant cover. As a result the dry lake vegetation data include one control transect, one transect under the wire of the 1937 powerline, and the vegetation under the two sets of pylons.

1937 Power Line

Vegetation sample data for the 1937 powerline are analyzed in Table 4. Total perennial ground cover for the 20 transects representing the 1937 powerline range from about 11 to 57 percent. Ground cover on control transects ranges from 11 to 13 percent except in study area 3 where it is 20 percent. Ground cover on the transect under the central wire is slightly higher than the control in the first three study areas, significantly higher in study area 4, and approximately the same in study area 5. Ground cover along the road edge is substantially greater than control values in all study areas and greater than under the central wire in four of the study areas. Total perennial ground cover under the pylons shows the greatest variation, ranging from considerably less than control values (area 3), to slightly above control values (area 2), to substantially above control values (area 1), and finally to over four times control values (area 4). In most study areas, the number of plants on transects A, B, and C are approximately the same while a two- to three-fold increase in plant number is evident in transect D under the pylons. The proportion of *Larrea* decreases under the pylons (transect D) as compared with the other three transects. Interestingly, the proportions of *Ambrosia* sometimes increase under the pylons and, in the first three study areas, decrease drastically under the central wire. The latter observation suggests that *Ambrosia* is easily decreased by trampling. Its increase under the pylon (study area 1) suggests that it has a greater pioneer capacity than does *Larrea*. All the long-lived perennials taken together show a pattern of high total ground cover on the first three transects and then a slight to moderate decrease on the transects under the pylon. A reciprocal relationship is evidenced by *Hymenoclea* and other short-lived perennials, namely, their presence in relatively small proportions on the first three transects and an increase in proportion of ground cover under the pylons. Finally, the Community Quality Index for the 20 transects ranges from 32 to 57 (Table 4). Generally the control transect has the lowest or very close to the lowest CQI for all five areas. Transects along the road edge and under the wire have CQI's at least as high as the control and in most cases higher, while transects under the pylons are the most variable with CQI values ranging from less than control (sample area 3) to substantially above control (sample area 4). These CQI values compare quite well with those of the ten reference transects (Table 2), which had values from 24 to 50 over a greater diversity of terrain.

1970 Power Line

An analysis of the vegetation sample data for the four study areas along the 1970 powerline (Table 5) indicates a range in total perennial ground cover between 1 and 48 percent. The most conspicuous pattern is a marked decrease in ground cover under the pylons (Transect D), while transects under the wire and at the road edge (B and C) generally have greater ground cover than the control. Approximately the same numbers

TABLE 4. ANALYSIS OF VEGETATION ALONG A POWER LINE CONSTRUCTED IN 1937. TR = transect; A = control; B = wire; C = road edge; D = pylon; GC = ground cover; LL = long-lived species; SL = short-lived species; CQI = community quality index.

TR	% Total GC	Density per 100 m²	Number of species	% of total GC provided by						CQI
				Larrea	*Ambrosia*	Other LL	Total LL	*Hymen-oclea*	Total SL	
Study area 1										
A	11.75	48.0	4	45.02	47.57	7.40	100.00	0.00	0.00	34.28
B	15.49	41.5	2	85.86	14.14	0.00	100.00	0.00	0.00	39.38
C	19.51	38.0	3	69.20	28.81	2.00	100.00	0.00	0.00	44.17
D	21.33	56.5	4	20.96	70.18	0.09	91.23	8.77	8.77	44.11
Study area 2										
A	11.13	38.5	3	44.20	54.09	0.00	98.29	1.71	1.71	33.08
B	17.18	36.5	5	77.59	20.90	0.93	99.42	0.58	0.58	41.33
C	16.85	40.0	2	70.33	29.67	0.00	100.00	0.00	0.00	41.09
D	11.59	62.5	4	39.86	50.22	0.00	90.08	5.78	9.92	32.31
Study area 3										
A	20.24	39.5	6	55.39	23.62	20.45	99.46	0.00	0.54	44.87
B	21.95	41.0	7	61.96	11.34	25.83	99.13	0.50	0.87	46.65
C	24.03	45.5	8	49.18	24.53	26.13	99.84	0.00	0.16	49.99
D	13.15	99.5	6	15.74	14.90	58.48	89.13	10.87	10.87	34.23
Study area 4										
A	13.23	17.5	11	70.21	7.16	19.68	97.05	0.00	2.94	35.87
B	29.98	49.0	7	41.76	8.74	37.16	87.66	0.00	12.34	51.26
C	32.55	42.5	15	45.41	2.12	38.46	85.99	2.15	14.01	52.91
D	57.18	128.5	11	23.15	1.63	32.77	57.56	10.49	42.44	57.37
Study area 5										
A	12.45	25.0	4	70.36	23.53	3.05	96.95	0.00	3.05	34.74
B	12.06	23.0	6	73.80	18.41	5.97	98.18	0.00	1.82	34.41
C	33.11	31.0	5	81.24	3.02	12.72	96.98	0.00	3.02	56.67
D	19.03	53.5	7	42.09	8.62	30.37	81.08	0.00	18.92	39.28

TABLE 5. ANALYSIS OF THE VEGETATION ALONG A POWEE LINE CONSTRUCTED IN 1970. Headings as in Table 4.

TR	% Total GC	Density per 100 m²	Number of species	% of total GC provided by						CQI
				Larrea	*Ambrosia*	Other LL	Total LL	*Hymen-oclea*	Total SL	
Study area 7										
A	25.55	62.5	4	81.53	14.91	3.56	100.00	0.00	0.00	50.55
B	15.97	52.5	3	63.56	35.94	0.50	100.00	0.00	0.00	39.96
C	35.46	62.5	4	67.18	31.84	0.00	98.96	0.82	1.04	59.24
D	8.94	35.5	3	41.39	54.25	0.00	95.64	4.36	4.36	29.24
Study area 8										
A	9.66	37.0	3	55.07	44.41	0.00	99.48	0.52	0.52	31.00
B	15.27	43.0	4	79.90	16.50	2.95	99.35	0.65	0.65	38.95
C	16.85	40.0	2	70.33	29.67	0.00	100.00	0.00	0.00	41.09
D	1.46	9.0	4	62.33	34.25	0.68	97.26	0.00	2.74	11.92
Study area 9										
A	20.24	40.0	6	55.39	23.62	20.45	99.46	0.00	0.54	44.87
B	22.77	45.0	9	69.78	15.33	14.40	99.52	0.00	0.48	47.60
C	25.03	45.5	8	49.18	24.53	26.13	99.84	0.00	0.16	49.99
D	9.27	88.0	5	17.48	17.04	65.48	100.00	0.00	0.00	30.45
Study area 10										
A	28.21	53.0	10	0.00	0.00	49.81	49.81	17.26	50.19	37.49
B	43.64	100.5	11	0.00	0.00	48.79	48.79	19.52	51.21	46.14
C	48.39	100.5	11	0.00	0.00	62.16	62.16	19.48	37.84	54.84
D	14.66	58.0	9	0.00	0.00	24.83	24.83	11.80	75.17	19.08

TABLE 6. ANALYSIS AND EVALUATION OF PLANT COVER SAMPLES FROM RABBIT DRY LAKE. (Study areas 6 and 10). TR = transect; A = control; B = wire; D = pylon; GC = ground cover; LL = long-lived perennials; SL = short-lived perennials; CQI = community quality index.

TR	Total GC %	Density per 100 m^2	Number of species	% of total GC provided by						CQI
				Atriplex confertifolia	*Atriplex polycarpa*	*Suaeda fruticosa*	Other LL	Total LL	*Atriplex lentiformis* (Total SL)	
A	17.09	47.0	7	55.65	6.09	21.30	16.99	100.00	0.00	41.34
B	16.05	67.5	5	47.48	9.22	32.02	11.28	100.00	0.00	40.06
(1937) D	10.42	16.0	4	31.67	0.38	43.67	0.00	75.72	24.28	28.09
(1970) D	9.76	63.5	6	43.75	36.48	1.95	0.41	82.58	17.42	28.49

of plants occur on the first three transects, except in study area 10 where transects B (wire) and C (road edge) have a greater number of plants and greater ground cover. On transect D (pylon) plant number decreases drastically in study areas 7 and 8 but increases substantially in study area 9 and remains just slightly above control levels in study area 10. The number of species observed on the several transects is about the same as for the other powerline. Long-lived perennials provide essentially all of the ground cover in all transects of the first three study areas. The virtual absence of pioneer species is rather surprising in view of their noticeable presence on the older powerline. However, the short period between completion of the powerline and the observations recorded in these data may have precluded the establishment of pioneer shrubs to any substantial degree. The long-lived plants under the pylons, then, may be residual; that is, the very large area covered by the new-style pylons on the 1970 line may not have required complete clearance for pylon construction as was probably the case with the older pylons. In any event, the proportion of short-lived species is relatively small, reaching over 4 percent only under the pylons in study area 7. Study area 10 deserves special mention here, because of the complete absence of *Larrea* or *Ambrosia* on any of the four transects. The long-lived species of the creosote bush scrub community comprise only about half the ground cover in this study area, which is located at the edge of the Joshua-Juniper scrub woodland and really not in a creosote bush scrub community. The Community Quality Index for each of the 16 transects (Table 5) ranges from approximately 12 to 59. Thus the range of CQI values is comparable to that of the 1937 powerline, except CQI values for the vegetation under pylons are substantially lower, indicating severe disturbance by pylon construction.

Alkali Sink Vegetation

The vegetation in the salt bush scrub community of the alkali sink at Rabbit Dry Lake (areas 6 and 11) has several interesting and noteworthy aspects. First, the control transect and the transect under the central wire of the 1937 powerline (Table 6) are quite comparable with respect to total ground cover, number of species, proportion of ground cover provided by a major long-lived species, the absence of ground cover provided by short-lived species, and the CQI. They differ slightly in the number of plants per 100 m^2 area. The two transects comparing vegetation under the pylons of the 1937 and the 1970 powerlines are closely similar and stand in contrast to the two other transects. The two pylon transects are comparable with respect to the total perennial ground cover, the number of species present, the proportion of ground cover provided by *Atriplex confertifolia,* the total ground cover by all long-lived species, the ground cover provided by *Atriplex lentiformis* (short-lived species), and the CQI. The two transects differ somewhat in that the vegetation under the 1937 pylons comprises a few large plants while the

vegetation under the 1970 pylons is made up of a large number of small plants. Another striking difference is that *Atriplex polycarpa* is sparingly present under the 1937 pylons, yet comprises 36 percent of the ground cover under the 1970 pylons. In contrast, *Suaeda fruticosa* contributes 43 percent of the ground cover under the 1937 pylons and only 1.95 percent under the 1970 pylons. Both are present with intermediate ground coverages in the control transect. A strong pioneer role under the 1970 pylons near Lucerne Dry Lake (area 3) suggests that *Atriplex polycarpa* (cited in Table 4 under "other LL") may have a more definite pioneer role in a salt sink situation than it does elsewhere. In any event, the successional status, the age span characteristics under different environmental conditions, and the general ecophysiological response patterns of *Atriplex polycarpa* need further study. Some of the puzzling circumstances might possibly be explained, if we knew the season in which pylon construction was completed and germination conditions (i.e., rainfall) became favorable. In the absence of that information, further attempts at explanation are not warranted.

Discussion and Evaluation

Evaluation of the impact of powerline construction and operation may be approached in several ways. Visual scanning of Tables 4 and 5 shows that plant number increases on the old powerline and usually decreases on the new powerline with increased disturbance and that the proportion of ground cover provided by short-lived perennials is usually higher on sites of severe disturbance (under pylons).

A second approach to the evaluation of the impact of powerline construction involves comparisons of the Community Quality Index among several transects. Community Quality Indices for the two powerlines are accumulated in Table 7 for comparison. The apparent pattern for the 1937 line is that the central wire transect has a substantially higher CQI than does the control, except in study area 5. Additionally, transect C at the road edge has a CQI higher than transect B, and is also higher than transect A, except in sample area 2. Greater variation is evident under the pylons where the CQI may be highest (area 4), approximately as high as the road edge transect (area 1), an intermediate value (area 5), approximately equal to control level (area 2), or considerably below control level (area 3). On the average, however, the CQI for transect D (pylons) approximates that of transect B and remains somewhat above the control level. The greater range of variation in transect D, again, is notable.

Similar analysis for the 1970 powerline also shows the pattern of increasing CQI through transects A, B, and C, except in study area 7 where the control transect registered an unusually high CQI due to high ground cover. Except for the high CQI in area 7, the pattern for A, B, and C closely approximates that for the 1937 line. With regard to transect D, under the pylons, a considerably lower CQI is registered in every

TABLE 7. COMMUNITY QUALITY INDICES FOR VEGETATION SAMPLES ALONG TWO POWER LINES. Areas 1–5 1937 line; areas 7–9 1970 line; A, control; B, wire; C, road edge; D, pylon;

$$CQI = \sqrt{\% \text{ total perennial cover} \times \% \text{ of total perennial cover by long-lived species}}$$

Area	Transect				Area	Transect			
	A	B	C	D		A	B	C	D
1	34.28	39.38	44.17	44.11	7	50.55	39.96	59.24	29.24
2	33.08	41.33	41.09	32.31	8	31.00	38.95	41.09	11.92
3	44.87	46.65	49.99	34.23	9	44.87	47.00	49.99	30.45
4	35.87	51.26	52.91	57.37	10	37.49	46.14	54.84	19.08
5	34.74	34.41	56.67	39.28					

study area, averaging only about half that of the control level. From these comparisons, a general and probably significant increase in the CQI is evident in the vegetation under the central wire and at the road edge. The vegetation under the pylons 33 years after disturbance is quite variable, having a quality ranging from lower than the control to higher than the control. However, only a few years after disturbance, the quality (CQI) of the vegetation under the pylons is consistently very low. At this point, stands of vegetation may be judged to be better or worse than other stands in terms of ecological quality by comparing CQI values.

The effects of the several treatments, as represented by the four different classes of transects, appear to be significant. But inspection of Table 7 suggests some differences in the levels of CQI from one study area to another, in addition to some differences between samples on the two powerlines within a given study area. To sort out these possible effects, a three-way analysis of variance (Sokal and Rohlf, 1969) was undertaken for the CQI values listed in Table 7. Since greater convenience of computation is permitted by having equal numbers of entries in the data matrix, the four study areas of the 1970 line were compared with only four of the study areas of the 1937 line. Study area 5, rather than study area 4, of the 1937 line was selected for comparison with study area 10 of the 1970 line because it was judged more comparable. A first analysis of variance compared four study areas in each of the two powerlines (1, 2, 3, 4 vs. 7, 8, 9, 10) and then, because the two powerlines run together only through three study areas, a second analysis of variance compared only the data from three study areas (1, 2, 3 vs. 7, 8, 9) on each powerline in a 2 by 3 by 4 data matrix. Results of those two analyses of variance are shown in Table 8. The patterns are similar in both

TABLE 8. THREE-WAY ANALYSIS OF VARIANCE FOR CQI VALUES IN TABLE 7. MS = mean square; F = variance ratio; Sig. = relative significance; NS = not significant; *, **, *** = significance respectively at the 0.05, 0.01, and 0.001 levels of probability.

Source of variation	Four Sample Areas			Three Sample Areas		
	MS	F	Sig.	MS	F	Sig.
Main effects						
A—power lines	32.87	1.16	NS	4.70	.....	NS
B—transects	522.44	18.42	***	311.37	13.27	**
C—study areas	153.64	5.42	*	230.15	9.81	*
First order interaction						
A X B	17306.24	610.66	***	12916.29	550.80	***
A X C	17176.39	606.08	***	19268.92	821.70	***
B X C	5746.28	202.76	***	6429.57	274.18	***
Second order interaction						
A X B X C	28.34	.....	.....	23.45	.....	.....

analyses and can be discussed as one. As a direct source of variation among CQI values (Table 8), the two powerlines are not significant. Differences attributable to the several study areas, however, are significant ($p < 0.05$). The direct effects attributable to the different transects are significant at the 1 percent probability level for the three sets of paired study areas and at the 0.1 percent level of probability for the four study areas. Of great interest, however, is that the first order interaction between any two pairs of variation sources is highly significant at the 0.1 percent level of probability in both analyses. We interpret the direct effects to mean that the vegetation of the two powerlines is the same, even when combining all the variations from all sources into one comparison. We also interpret the variation between study areas to be significant, but not overriding; but, the variation among transects (or treatments of the vegetation due to powerline construction and operation) is large and highly significant. We interpret the first order interaction results to mean that disturbance of something as complex as vegetation has highly significant effects, far greater than would have been predicted from separate consideration of the individual factors, and that response to treatment differs with regard to both space and time. These analyses of variance, therefore, confirm and extend the conclusions reached by other approaches. Namely, the greater disturbance associated with pylon construction imparts a greater variation and hence lack of predictability to vegetational response than does less severe disturbance such as trampling under the central wire.

In general, then, the effect of the construction and operation of transmission powerlines is one of a slight enhancement of the vegetation, i.e.,

an increase in cover under the central wire, somewhat greater enhancement of the vegetation along the road edge, and a highly variable response of the vegetation under the plyons. Reasons for enhancement of the vegetation under the central wire are conjectural at this time. However, one possibility is that moisture from clouds, fog, and rain may be concentrated toward the low point of the sagging wire and there drips off to the ground. Explanations for the enhancement of vegetation at the road edge are probably two. One involves drainage off the road or road edge accumulation of ordinary down-slope drainage. However, our observations indicate enhancement of road edge vegetation also occurs in areas where such obvious drainage factors do not apply. The second explanation involves removal of competition by plants that formerly were located on the roadway. Whether other factors pertain is at this point problematical.

Reasons for the decrease in vegetation under the pylons are of course related to mechanical removal or drastic disturbance during construction. Revegetation occurs to the extent that after 33 years disturbance effects are still detectable, but the quality of the recovering vegetation approaches that of the surrounding vegetation. Variability is greater than that of the surrounding vegetation, suggesting low predictability concerning the time course of vegetative recovery. The reasons for low predictability are perhaps several and may relate to such factors as the thoroughness of mechanical removal, the depth of soil disturbance, and the species that happen to be the first invaders. The latter, in turn, may have been influenced by seasonal and climatic conditions at the time disturbance ceased, and by the seed source available for invasion. We suspect a different course of succession would follow depending upon whether initial pioneer invasion occurred following summer, versus winter, rain. Predictability probably also depends upon the age span of the particular pioneer species that happened to colonize a given pylon site. Clearly plants like *Eriogonum fasciculatum* or *Atriplex polycarpa* would be longer-lived pioneers than plants like *Euphorbia polycarpa* or *Stephanomeria pauciflora*. The need for more careful definition of relative age span is obvious. In any event, predictability following the fairly drastic disturbance of pylon construction is relatively low.

The overall and long-term effects of powerline construction and operation, then, are: a permanent legacy of a devegetated maintenance road; variable, but fairly regular, road edge enhancement of vegetation; slight enhancement of vegetation between power pylons; and a drastic disturbance immediately under the pylons from which vegetation recovers significantly but not completely after about 33 years.

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ADDITIONS AND CORRECTIONS TO A REVIEW OF NORTH AMERICAN PACIFIC COAST BEACH VEGETATION

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Breckon and Barbour (1974) recently reviewed the literature on beach vegetation of the Pacific Coast of North America. Subsequent field observations verified many of their conclusions about structure and distribution of beach communities and revealed new information requiring corrections and reconsideration of some of their conclusions. Our survey ranged from Washington (approximately 48° N latitude) to Cabo San Lucas, Baja California (23° N).

For the sake of brevity, additions, corrections, and deletions for the list of characteristic beach species are summarized in text. The interested

reader can transfer these changes to Table 2 in Breckon and Barbour pages 342–4. Of the 22 taxa listed below, six represent additions, four are deletions, and the rest show modifications in range or nomenclature or both.

The new taxa are narrowly restricted with ranges of less than 5° latitude. Yet, within their ranges they all may be locally abundant and deserve to be recognized as characteristic beach taxa.

Three deleted species, *Lycium brevipes, Salicornia subterminale,* and *Suaeda californica,* have Baja California distributions, and Johnson has determined that they are more characteristic of salt marshes and shingle beaches than of the sandy beaches with which we are here concerned. The fourth deletion, *Tanacetum camphoratum,* has a very narrow beach distribution according to herbarium records (1°). We have been unable to relocate it along the coast and suggest that it is extinct in the beach habitat.

Changes in northern (N) or southern (S) limits for the other taxa, and complete nomenclature and range limits for the new taxa (*), are as follows:

Elymus mollis, S:35°

Cakile edentula, S:39°30′

Lathyrus littoralis, S:34°30′

**Elymus* ×*vancouverensis* Vasey (pro sp.), Maritime Endemic, nothomorph *californicus* Bowden, Maritime Endemic: N limit 50°, S limit 46°

**Ammophila breviligulata* Fern., Temperate Strand-E.N.A., Introduced: N limit 48°30′, S limit 46°

Polygonum paronychia, S:35°

Ambrosia chamissonis ssp. *cuneifolia,* N:47°30′, S:46°30′

**Agoseris apargioides* (Less.) Greene, Inland-Maritime Endemic: N limit 42° (47° in non-beach habitat), S limit 36°30′

Heliotropium curassavicum ssp. *oculatum,* S:22°53′

Mesembryanthemum chilense, S:30°

**Atriplex patula* L., Widespread Inland-Maritime, ssp. *hastata* (L.) Hall & Clem., Widespread Inland-Maritime: N limit 41°, S limit 40°40′

Atriplex leucophylla, N:39°30′, and change distribution type to Maritime Endemic

Abronia maritima, S:22°53′

**Malacothrix incana* (Nutt.) T. & G., Maritime Endemic: N limit 35°30′, S limit 34°

Camissonia cheiranthifolia ssp. *suffruticosa,* S:30°

Distichlis spicata, N:34°30′ (50° in non-beach habitat)

Sesuvium verrucosum, change distribution type to Widespread Inland-Maritime

**Diodia crassifolia* Benth., Maritime Endemic: N limit 22°54′, S limit 22°53′.

These floristic additions and subtractions and range adjustments are relatively minor, but they do affect Sorensen coefficients of community (K) and the location of provisional boundary segments (PBS's). De Jong recalculated K values for every 30′ segment and selected PBS's at latitudes where K values fell rather suddenly (indicating sudden floristic changes).

When these data are transferred to a map, the Pacific Coast of North America can be broken down into nine eco-floristic zones and subzones (fig. 1). Figure 1 in this paper corresponds to Figure 4 in the Breckon and Barbour article; several changes are apparent. The boundary between North Coastal and Mediterranean subzones within the Temperate

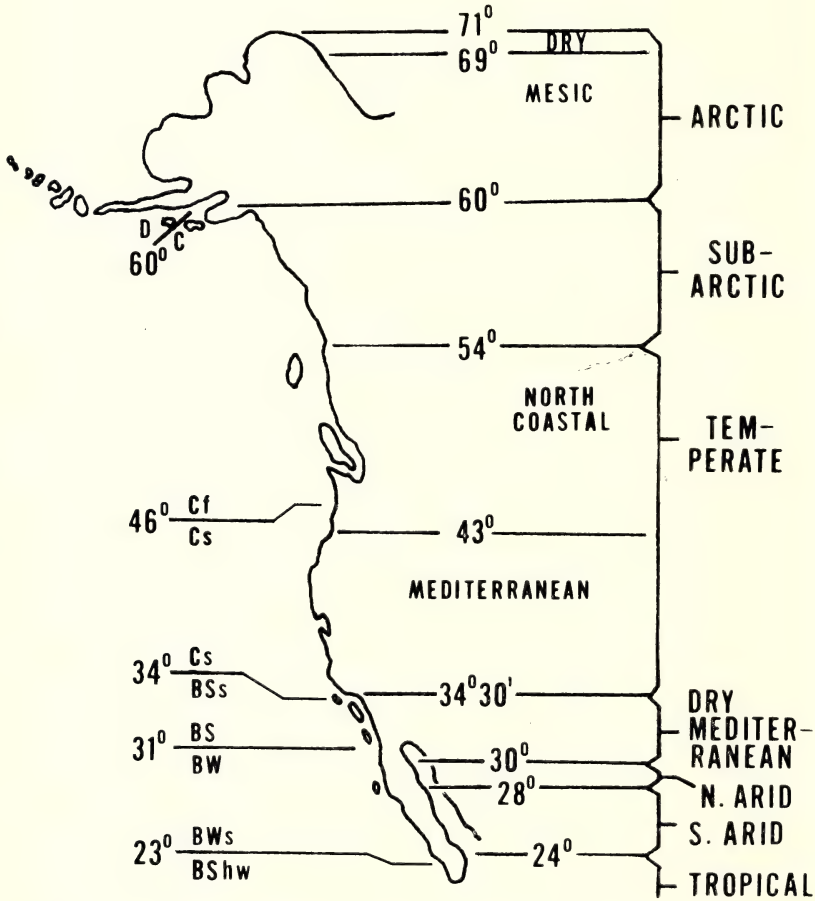

FIG. 1. Pacific Coast eco-floristic zones and subzones and major climatic boundaries (Koeppen system).

zone has been shifted south 30′. This is a minor change and does not correlate any better with a climatic shift at 46° than did the old boundary. That is, the floristic shift at 43° is still anomalous.

Changes to the south are more significant. The boundary between Temperate and Dry Mediterranean zones has been moved 2° south to 34°30′, near Point Conception, California. Eight taxa reach their southern limit between 35° and 34°. This new boundary now closely corresponds to a more general floristic boundary recognized by Stebbins and Major (1965). It also correlates well with a climatic shift from Cs (mesothermal) to BSs (semi-arid) climates at 34°. Breckon and Barbour (1974) had drawn the climatic boundary at 37° due to an error in their calculations. The shift to 34° more or less agrees with a map by Durrenberger (1965) that shows BS beginning at 35°45′. Using a precipitation/evaporation index, Thornthwaite (1941) found Point Conception (34°30′) to be a significant climatic boundary: in wet years it separates Cd (dry subhumid) from D (semi-arid) climates; in dry years it may separate D from E (arid) climates. In addition, both Durrenberger and Russell show the southern boundary of the fog zone (CsBn) to be around 35°20′. Thus, one may assume that a major climatic shift occurs between 35°20′ and 33°45′, and our eco-floristic boundary at 34°30′ is well within that region.

Another major change in location of the eco-floristic boundaries is that the dividing line between Dry Mediterranean and Northern Arid zones has been moved south 2°30′ to 30°. This now agrees closely with a 30°30′ southern boundary of the California floristic and faunal provinces proposed by Howell (1957) and Van Dyke (1919, 1929). It also roughly corresponds to a climatic shift from BS (semi-arid) to BW (arid) climates at 31°.

As a result of these boundary shifts, the Northern Arid zone is now quite constricted, occupying only 2° of latitude. This is probably an artificial zone, an artifact of a cliffed coast in that latitude with few and narrow beaches and minimal field work on our part. It does not correlate with any climatic peculiarities. Perhaps it might best be thought of as an ecotone region or as part of the Southern Arid zone, but we have chosen to retain the Breckon and Barbour zone name.

Finally, the region between 24° and 23°30′ was categorized as an ecotone by Breckon and Barbour, but we believe its affinities are definitely tropical and so have combined it with the Tropical zone. The northern edge of the Tropical zone correlates closely with a climatic shift at 24° from BWs (arid, summer drought) to BShw (semi-arid, warm, winter drought). Breckon and Barbour had previously placed the tip of Baja California in Aw (tropical, winter drought) by error.

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SYNTHETIC HYBRIDIZATION AND TAXONOMY OF WESTERN NORTH AMERICAN DICHANTHELIUM, GROUP LANUGINOSA (POACEAE)

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Dichanthelium has been recognized to differ from the bulk of *Panicum* since 1910 when Hitchcock and Chase described it as a subgenus containing nearly 120 species. Recently elevated to generic rank (Gould, 1974), it differs from *Panicum* by morphological, anatomical, and cytological characters, and by having a C_3, rather than a C_4, photosynthetic pathway (Clark and Gould, in press). In contrast to the widespread pantropical and warm temperate *Panicum, Dichanthelium* occurs in a geographically limited area, being mostly North American, a few species ranging into the West Indies and to northern South America. Whether it is a recent or ancient derivative from basic panicoid stock presently cannot be ascertained. However, the several kinds of differences between one genus and the other, although each difference alone is possibly not of significance for generic segregation, when taken together indicate natural phyletic units. Even though only a small morphological gap separates *Dichanthelium* from *Panicum,* the segregation can be justified since the two resultant genera are natural and remain large, meeting the recommendation of the inverse ratio between the size of genera and their intervening gap (summarized by Mayr, 1968, pp. 234–238).

The early part of this paper uses *Panicum* nomenclature rather than that of *Dichanthelium* since literature using the former is so widely available. The dichanthelium panicums are notorious for the taxonomic difficulties that arise when one attempts to delimit species, and as a result taxonomic treatments vary from extreme "splitting" to extensive "lumping" (Shinners, 1944). Within subg. *Dichanthelium,* Hitchcock and Chase (1910) aggregated the numerous species into 17 taxonomically informal groups. One of these, group Lanuginosa, has only three common, traditionally recognized species in western United States, *P. occidentale* Scribn., *P. pacificum* Hitchc. & Chase, and *P. thermale* Bol. (Hitchcock, 1951; Hitchcock and Chase, 1910). These three species plus a fourth in the group Oligosanthes, *P. scribnerianum* Nash, present a much simpler situation in the West than in eastern United States where the bulk of the species occur; however, the patterns of variation seen in the West and the kinds of taxonomic problems evident, although less complex, seem to mirror those of eastern members of the genus. Lelong (1965) and Spellenberg (1975) have demonstrated that at least part of the taxonomic problems with these grasses results from a high incidence of autogamy combined with occasional successful outbreeding.

Early taxonomists generally applied to the western forms names now used for eastern species (cf. Spellenberg, 1968, for a complete review). Among the most commonly used was *Panicum dichotomum* L., considered by Watson (1880), Vasey (1885), and Jepson (1911) to refer to a variable species. *Panicum pubescens* Lam. or Michx. is also a name applied to most of the species in the Lanuginosa group at one time or another (Hitchcock and Chase, 1910). From about 1860 to 1910 several of the western Lanuginosa forms were described as species separate from eastern ones, and four of these, *P. thermale, P. occidentale, P. shastense* Scribn. & Merr., and *P. pacificum,* were recognized by Hitchcock and Chase (1910). They also reported the eastern species *P. huachucae* Ashe and *P. tennesseense* Ashe to have a few outlying populations in Colorado, Utah, and Arizona.

Panicum thermale, P. pacificum, and *P. occidentale,* as recognized by Hitchcock and Chase (1910) and Hitchcock (1951), were said to differ mainly by vestiture, particularly that of the adaxial surfaces of the blades. *Panicum thermale* is "velvety-villous", *P. pacificum* is "pilose", and *P. occidentale* (especially the blades) is nearly glabrous (Hitchcock, 1951). The nature of the pubescence does not change when plants are brought from the field and grown under uniform greenhouse conditions, removing the possibility that the quality and quantity of pubescence respond directly to ecological conditions. The intergradation between these forms and variation in the habit of plants, a feature also used to distinguish *P. pacificum* from *P. occidentale,* are discussed in the taxonomic section. The species show virtually no geographic separation (fig. 1), and the stated ecological differences recorded in the literature

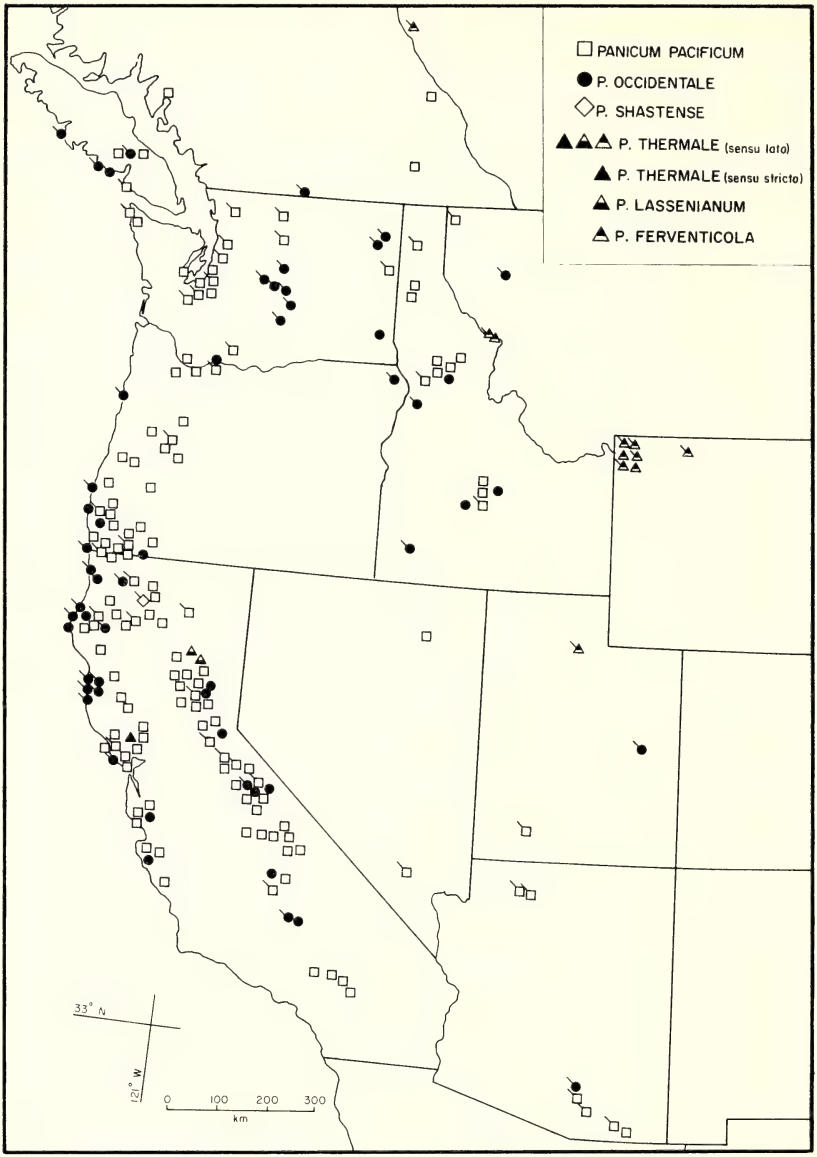

FIG. 1. Distribution of *Panicum,* group Lanuginosa in western North America, following nomenclature of earlier classifications. Rays on the upper left of some figures represent plants with the largest spikelets less than 1.8 mm long.

are non-existent when the species are examined over their entire ranges.

Although Hitchcock and Chase's treatment (1910) was followed in most western floristic works for the next 60 years, a few authors chose to recognize fewer species. Fernald (1921), noting intergradation be-

tween the members of the eastern portion of the complex, included *P. pacificum* in an enlarged and variable *P. lindheimeri* Nash. In 1934, he included this under *P. lanuginosum,* broadening the species even further. Floristic treatments using similarly broad and inclusive species concepts have been produced for the eastern United States (e.g., Gleason, 1952; Pohl, 1947). Spellenberg (1969) indicated that the western forms might not be separable from eastern species but maintained all those from the West under the oldest northwestern name, *P. occidentale,* excluding the population of *P. thermale* from Sonoma Co., California. Schmoll (1939), in her study of *Panicum thermale,* chose to recognize more species in the West than those recognized by Hitchcock and Chase. She noted that plants from (1) The Geysers, Sonoma Co., California, (2) Lassen Volcanic National Park, California, and (3) Yellowstone National Park, Wyoming, and Banff, Alberta, formed three more or less distinct groups, which she named *P. thermale, P. lassenianum,* and *P. ferventicola,* respectively. Her treatment reflects the morphological differences between populations previously regarded as one species and certainly obviates the problem of how *P. thermale* (sensu lato) attained such a geographic distribution (fig. 1). However, the recognition of these populations each at the specific level seems artificial when one considers the numerous intergrading forms occurring in the closely related species, *P. pacificum* and *P. occidentale,* from nearby, non-hydrothermal areas.

In attempting to separate western species from closely related eastern ones, especially *P. huachucae, P. tennesseense,* and *P. lanuginosum* Ell., Hitchcock and Chase (1910) used such features as the autumnal habit (due primarily to the extent and region of branching on the culms), quality and quantity of pubescence, and spikelet length. However, even a cursory examination of plants in the field and of herbarium specimens indicates that the vegetative features mentioned are variable and will not serve alone or in combination to separate species. There is a tendency then to rely on the easily measurable length of the spikelets. *Panicum huachucae* and *P. tennesseense* have spikelets 1.6–1.8 mm long, whereas *P. occidentale* and *P. pacificum* have spikelets 1.8–2.0 mm long. Plants of the eastern species rarely have spikelets exceeding the range stated, but western plants commonly have the largest spikelets less than 1.8 mm long (fig. 1), a fact that has been consistently overlooked. They would be identified as eastern species if the geographic origin of the collection were not known.

As numerous authors of eastern floras have noted, *P. huachucae* intergrades with the southeastern United States *P. lanuginosum* and there is an increasing tendency to use the latter name for all these closely related forms. *Panicum huachucae* differs somewhat in its more erect habit and by its "short-pilose" adaxial blade surfaces, whereas *P. lanuginosum* is "velvety-villous" (Hitchcock, 1951), but in eastern Texas and for some collections from the Southeast the distinction is moot.

In an attempt to understand the possible interrelationships among the western populations of these grasses and also between eastern and western species, a series of synthetic hybridizations was made. These are reported below. Chromosome numbers are reported in Table 1, and morphological characteristics are discussed in the taxonomic section. Additional chromosome counts, a study of phenolic compounds (not identified) by paper chromatography, and studies of leaf anatomy were also made, but none of these techniques (fully reported in Spellenberg, 1968) produced a means of differentiating between the western species as traditionally recognized.

TABLE 1. GEOGRAPHIC ORIGIN, CHROMOSOME NUMBER, AND SPECIMEN VOUCHERS OF DICHANTHELIUM USED IN HYBRIDIZATION EXPERIMENTS IN THIS STUDY. *Panicum* nomenclature of Hitchcock, 1951, is followed for ease in comparison to Figures 2 and 3. Collection numbers are the author's unless otherwise noted. Vouchers are deposited at WTU, partial sets at NY and NMC.

P. huachucae, $n = 9$
New York, Bronx, New York Botanical Garden, rock outcrop, progeny grown from seed from *2158*.

P. lanuginosum, $n = 9$
Alabama, Baldwin Co., 3 mi SW of Bay Minette on U. S. Highway 31, in woods, progeny grown from seed from *1862*.

P. lindheimeri, $n = 9$.
Texas, Brazos Co., 2 mi E of College Station, *F. W. Gould 11957*.

P. occidentale, $n = 9$
Idaho, Custer Co., 10 mi W of Clayton, Sunbeam Hot Springs, *316;* Owhyee Co., 10 mi SE of Bruneau, Hot Creek Falls, *318,* (near *P. brodiei*).
Washington, Chelan Co., Peshastin, river bank *1438,* (glabrous phase).

P. pacificum, $n = 9$
British Columbia, Kootenai District, Fairmont Hot Springs, *1189*.
California, Del Norte Co., Gasquet, in open woods along road, *603;* Shasta Co., Castle Crags, at old logging landing, *617;* 1 mi W of Redding on Calif. Highway 299, creek bed, *2116;* between head of Whiskeytown Lake and French Gulch along California Highway 299, creek bank, *2137*.
Idaho, Elmore Co., Atlanta, bare warm dirt, *512;* Idaho Co., 10 mi E of Lowell on banks of Lochsa River, *1489*.
Montana, Lincoln Co., 3 mi NW of Troy on Kootenai River, *1498*.
Oregon, Lane Co., Belknap Hot Springs, *1600*.
Washington, Pierce Co., 4 mi S of Spanaway, open gravelly ground, *1499;* along Interstate 5 at Steilacoom Exit, *2133;* Snohomish Co., Sultan, borrow pit near river, *1526;* 2 mi E of Gold Bar in sandy opening near river, *2131*.

P. tenneesseense, $n = 9$
Ontario, Norfolk Co., Long Point Park, *J. S. Pringle, s.n.*

P. thermale, $n = 9$
California, Lassen Volcanic National Park, Sulfur Works, mineralized soil, *472;* Sonoma Co., The Geysers, *402, 1307*.
Wyoming, Yellowstone National Park, Mammoth, *529;* 5 mi N of Norris, edge of warm stream, *532;* Roaring Mountain, *535*.

Synthetic Hybrids

Synthetic hybrids were made by techniques described in Spellenberg (1975). Hybrids were easy to obtain in most combinations; more than 1100 individual cross pollinations were attempted in about 50 combinations. Data regarding hybrid seed set and hybrid seed germination (reported in Spellenberg, 1968) are not considered particularly relevant for ascertaining the degree of relationship between populations for several reasons: (1) because of the small size of the spikelets, damage to the gynoecium often occurred when anthers were being removed from the opening floret prior to cross pollination; (2) the crossing process is tedious and often very few individual flowers were crossed, producing only a small sample of crossed florets; (3) plump, field-collected seed commonly have a low frequency of germination under greenhouse conditions, most seeds from some populations apparently requiring some unknown combination of factors prior to germination (Lelong, 1965; Spellenberg, 1968). These points in combination may account for the few crosses where no hybrids were obtained. The unsuccessful crosses were between populations that did not differ morphologically from one another more than those that produced successful crosses and are much more similar than *P. pacificum* and *P. scribnerianum* Nash between which successful crosses were made (Spellenberg, 1970). Thus the discussion regarding synthetic hybridization is restricted only to those crosses that produced F_1 progeny.

In all but one of the crosses, progeny were vigorous, flowered normally the first summer after winter germination, and were intermediate between the parents in morphology and time of initial onset of flowering (if this differed in parents) under greenhouse conditions. One exception to this was the progeny from the cross *P. pacificum* (Ida., Atlanta, *512*) × *P. thermale* (Yellowstone, *532*). (The seed parent is presented first in all crosses discussed; collection numbers are the author's). The 26 seedlings were very weak and difficult to establish; 14 were grown for nearly six months but all produced very small weak plants; the two most robust were kept for 2.5 years. None flowered but instead appeared much like diminutive, densely fascicled winter rosettes. Both parent plants used in this cross produced normal progeny when crossed with other populations.

Meiosis in hybrids was examined by standard techniques reported elsewhere (Spellenberg 1970; 1975). Parent plants consistently formed nine normal-appearing bivalents and in the F_1 hybrids, where an attempt was made to examine at least 50–100 meiocytes, only 2–20 percent of the meiocytes exhibited abnormalities such as univalents, lagging chromosomes or fragments, anaphase bridges, and micronuclei or rarely microcytes. Higher frequencies of irregularities were noted in the progeny from a few crosses. Parents of *P. thermale* (Mt. Lassen Nat. Pk., *472*) and *P. occidentale* (Ida., Owhyee Co., *318*) carried large translocations

and in progeny from two crosses produced up to about 50 percent abnormal meioses (Spellenberg, 1975). In a cross involving *P. lanuginosum* (*1862*) and *P. pacificum* (*2116*), 40 percent of the metaphase I figures showed lagging chromosomes, but later stages were normal. No greater or lesser percentage of meiotic abnormality could be correlated with traditional taxonomic delimitation of western species, but rather a local population apparently may accumulate a number of chromosomal differences that appear in hybrid meioses. This is illustrated by three intraspecific crosses in *P. pacificum* (cf. fig. 2). In the cross *2137* × *2116* (from California, 21 km apart), of 60 metaphase I meiocytes viewed, eight had a lagging univalent, but of 38 telophase I cells only two showed micronuclei. In *2133* × *1231* (from Washington, 96 km apart), of 153 metaphase I meiocytes only one had a lagging chromosome. In *2137* × *1189* (from California and British Columbia, 1280 km apart), of 65 cells viewed at diakinesis or metaphase I, no abnormalities were noted, and of 83 cell pairs at telophase I, all were normal.

Meiosis was examined in three of the trans-continental crosses (fig. 3). In *P. lanuginosum* (*1862*) × *P. pacificum* (*2116*) diakinesis generally appeared normal, but of 30 metaphase I figures examined, 11 had single lagging chromosomes and three had two lagging chromosomes. However, in this cross the 35 telophase I pairs of cells examined appeared normal. In the cross *P. lanuginosum* (*1862*) × *P. huachucae* (*2185*), of the 57 metaphase I meiocytes examined, only four had lagging univalents; few telophase I stages were seen, 11 were normal, and of the numerous telophase II cells scanned, about 2 percent had a small micronucleus. In the cross completing this triangle, *P. huachucae* (*2158*) × *P. pacificum* (*2116*) all 49 metaphase I cells viewed apeared normal, and all 95 telophase I cell pairs examined were normal except for remnants of an anaphase I bridge in three. Meiosis in these crosses and all others examined indicate a high degree of homology among the genomes of these species.

Fertility of parent and hybrid plants was estimated by immediately staining pollen from mature undehisced or dehiscing anthers of living plants in a solution of lactophenol-cotton blue. Evenly swollen and stained grains were considered normal; blotchy and smaller ones or those that were shrunken and non-staining were considered nonviable. Pollen from parent plants was generally 85–100 percent evenly stained and rarely was smaller and unevenly stained as it commonly was in the hybrids. Percentages are based on samples of 200 grains. The results are illustrated in Figures 2 and 3; where more than one count was obtained, a range is given. In some individual hybrids the percentage of stainable pollen varied little from count to count; in others variation was relatively large. A few of the parent plants had a comparatively low frequency of evenly staining grains: *P. pacificum* (*1189*) (63–75%), *P. thermale* (*402*) (63–76%), *P. thermale* (*472*) (74–

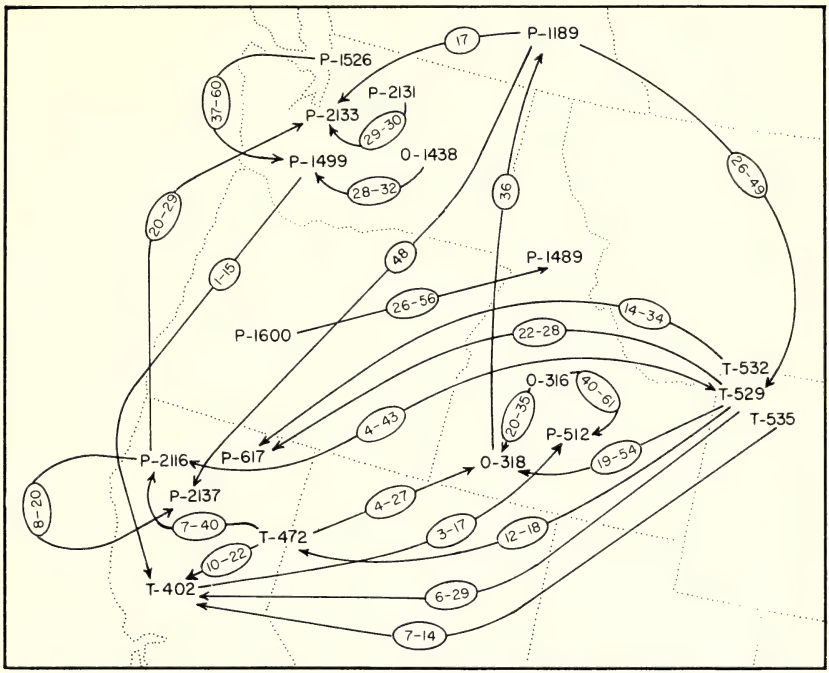

FIG. 2. Summary of synthetic hybridizations between western North American populations of *Dichanthelium lanuginosum*. P, O, and T preceding collection numbers refer to *Panicum pacificum*, *P. occidentale*, and *P. thermale* respectively. Arrows indicate cross, head of arrow points to seed parent, numbers in oval refer to percentage of stainable pollen in hybrid.

94%). In most instances in the hybrids, pollen viability is considerably less than would be estimated by abnormal meioses alone and the lower fertility must be attributed to genetic differences that are not observable at meiosis. There appears to be a weak tendency for hybrids to be of lower fertility as geographic distance between the parent populations increases, regardless of the plants involved in the cross, as long as crosses remain within the group Lanuginosa (cf. intergroup hybrids in Spellenberg, 1970), or are between closely related groups (*P. lindheimeri* in Figure 3 is in group Spreta). Interfertility between eastern and western species is not lower than between many western populations. It is also notable that all the *P. thermale* (sensu lato) populations when intercrossed show as low or lower fertility in hybrids than many interspecific western crosses, arguing, possibly, for independent origin or long separation of each of the *P. thermale* populations.

As Spellenberg (1975) demonstrated for progeny from a few crosses in these grasses followed to the F_3 generation, fertility in some lines returns to normal (85–100%). These highly fertile progeny slightly differ morphologically from each of the parents. They may also be

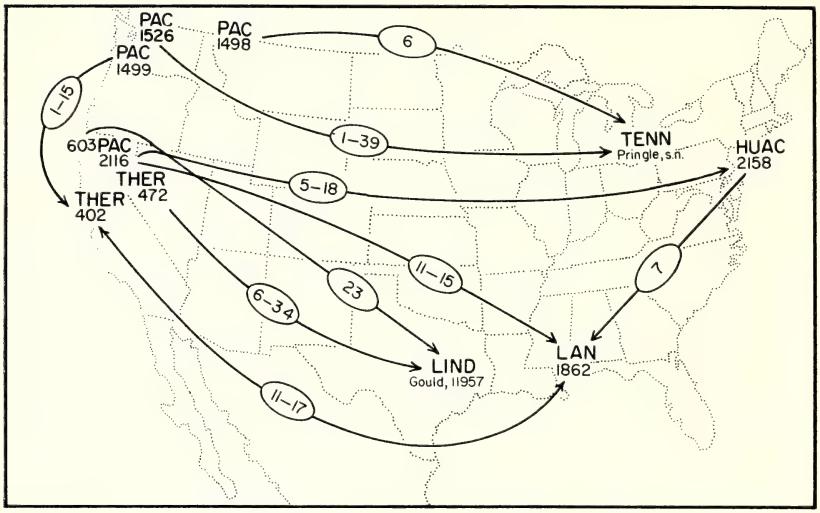

FIG. 3. Summary of transcontinental crosses in *Dichanthelium,* mostly group Lanuginosa. Under traditional treatment: HUAC = *Panicum huachucae;* LAN = *P. lanuginosum;* LIND = *P. lindheimeri* (in group Spreta); PAC = *P. pacificum;* TENN = *P. tennesseense;* THER = *P. thermale.* In revised treatment all except *P. lindheimeri* are included in *D. lanuginosum.* Arrows indicate cross, head of arrow points to seed parent, numbers in oval refer to percentage of stainable pollen in hybrid.

expected to be at least partially reproductively isolated from the parent plants due to recombination of factors promoting intersterility (Grant, 1958, pp. 355–357). The complex pattern of morphological variation seen in *Dichanthelium* probably is due in part to the coupling of a primarily autogamous system of reproduction with occasional hybridization and presents the expected taxonomic problems (Lewis, 1963). I am interpreting this complex as many highly inbred populations, most populations accumulating larger or smaller genetic differences, causing partial reproductive isolation between the populations. The most strongly isolated populations might be considered microspecies; few, however, are morphologically distinct. The overall variation seems minor, often even trivial, and to be about the same as that seen in many widely distributed xenogamous species. Following Lewis' (1963) suggestion for such groups, and following other authors' leads in floristic works for portions of the eastern United States, I am combining all the western forms under one name, *Dichanthelium lanuginosum* (Ell.) Gould.

TAXONOMY

The generic name *Dichanthelium* is adopted for the remainder of this paper. Of the few species of *Dichanthelium* in the western United States, *D. oligosanthes* (Schult.) Gould var. *scribnerianum* (Nash) Gould

(≡ *Panicum scribnerianum* Nash) (group Oligosanthes) is distinguished from the rest by having the largest spikelets (2.9–3.5 mm long), shortest ligules (0.5–1.5 mm long), and adaxial surfaces of the blades glabrous. Nearly or completely sterile hybrids between *D. lanuginosum* and *D. oligosanthes* occur rarely in the West. They bear spikelets 2.4–2.7 mm long, which have not been observed to perfect seed, and have ligules 1.0–3.0 mm long. Those from one area have been named *Panicum shastense* Scribn. & Merr. (Spellenberg, 1970). All these hybrids can be separated only with difficulty from *D. lanuginosum* var. *villosissimum* (Nash) Gould (≡ *P. villosissimum* Nash) collected once along the Columbia River near Troutdale, Oregon (Spellenberg, 1971). (My inclination is to recognize this variety as a species but to do so requires a new combination in *Dichanthelium,* which I would rather leave to one more experienced with this eastern form.) The single known specimen of this variety from the West has short dense hairs on the adaxial surfaces of the blades and is sparingly branched. All the remaining small-spikeleted (1.6–2.0 mm) western United States forms are included in this treatment except for the southern California record of *D. lindheimeri* (Nash) Gould (=*P. funstonii* Scribn. & Merr.). *Dichanthelium lindheimeri,* placed in the separate informal group Spreta in *Panicum* by Hitchcock and Chase (1910), is closely related to *D. lanuginosum* and the two can be easily crossed (fig. 3). Some authors of eastern United States botany (e.g., Gleason, 1952) maintain that the former is merely a variety of the latter, whereas others (e.g., Gould, 1975) maintain them as distinct species. Again I beg the issue, requiring a greater familiarity with the morass of intergrading eastern forms.

DICHANTHELIUM LANUGINOSUM (Ell.) Gould, Brittonia 26:60. 1974. — *P. lanuginosum* Ell., Bot. S. C. and Ga. 1:123. 1816. HOLOTYPE: *Dr. Baldwin,* "Hab. Georg.", CHARL!

Tufted perennials, subglabrous to densely pubescent throughout, overwintering as a more or less well marked rosette of usually short, broad leaves relatively stiff in nature as compared with the vernal and aestival foliage; culms at first simple, (5)15–65(80) cm tall and bearing lanceolate to linear-lanceolate blades and a terminal panicle; branch culms arising at the nodes of the vernal culms, sometimes attaining their height, but usually much shorter, branching repeatedly and forming loose to rather dense fascicles of reduced leaves and branches; nodes usually with a dense ring of more or less ascending to slightly reflexed hairs 0.5–1.0 mm long and with a glabrous ring below; sheaths of the vernal leaves (1.5)3–7(9) cm long, averaging about half the length of the internodes; ligule (actually a "pseudoligule" immediately above the minute true ligule) a dense ring of hairs (2.5)3–4(5) mm long; vernal blades lanceolate or linear-lanceolate, erect, ascending, or more or less spreading, (2.5)5–10(13) cm long, (3)5–10(15) mm wide, the upper-

most reduced, the margins usually with pustulate-based cilia at least at the base of the blade; panicles of the vernal culms generally well exserted, open and more or less ovate, (3)4–9(13) cm long and about as wide, the axis usually pubescent, the lower branches spreading, ascending, or occasionally somewhat reflexed, the upper ascending; panicles of the shorter branch culms usually less strongly exserted, reduced, the smallest usually more or less included in the fascicles of leaves; spikelets of the terminal primary panicles (1.5)1.6–2.0(2.1) mm long, about 0.8–1.1 mm wide, those of the branch panicles slightly smaller, more or less obovate-elliptic, subobtuse, pubescent with hairs about 0.1 mm long; first glume ¼–⅓ the length of the spikelet, usually with a faint nerve, or occasionally also with two smaller lateral nerves; the upper margin irregularly truncate to subacuminate; second glume and lemma equal, 7–9 nerved, slightly shorter than the fruit at maturity; sterile palea about half the length of the sterile lemma, hyaline, broadly ovate-lanceolate, notched at the tip to deeply divided; fertile lemma chartaceous-indurate, glossy, subacute and occasionally with a small rounded apiculus, its inrolled margins clasping a palea of similar texture, the two structures enclosing the caryopsis at maturity; fruit (including the lemma and palea)1.5–1.7 mm long and about 0.9 mm wide; $2n = 18$. March through August.

Sandy lake margins or riverbanks, moist to rather dry prairies, open woods, or sometimes in marshy areas, common in disturbed ground, from sea level to about 1370 m, but ascending to 2280 m about hot springs in the western mountains, southern British Columbia to Nova Scotia, south to the Gulf States and southern California, extending into Mexico; introduced in Japan; sporadic in areas of low rainfall (western distribution; fig. 4).

This species is considered an assemblage of wholly intergradient forms previously recognized at the specific level on the basis of such features as density and distribution of pubescence, minute differences in spikelet length, and the nature of branching and habit of the culms. Pohl (1947), studying these grasses in the northeastern United States, placed all forms under *P. implicatum* Scribn., maintaining *P. lanuginosum* as a separate southeastern species, noting that the complex pattern of variation might not allow for the useful application of a subspecific category. In the treatment of the western species presented here, only the variants that combine morphological and ecological distinctness are recognized.

Key to the western varieties of *D. lanuginosum*

1. Culms usually less than 30 cm tall, stiffly ascending or spreading, in compact tufts; sheaths about ⅘ the length of the internodes or longer, often prominently papillose; blades generally less than 6 cm long, usually less than 8 times as long as broad, all except the very lowermost usually pubescent on the adaxial surface; about hot springs above 1370 m in the Rocky Mountains . 2. var. *sericeum*

1. Culms usually over 30 cm tall, ascending or spreading, often decumbent or sprawling, in loose bunches or dense tufts; sheaths usually about half the length of the internodes, the papillae generally not prominent; blades commonly longer than 6 cm, generally about 8 times their width or longer, from pubescent to glabrous on the adaxial surface.
   2. Plants densely clothed with fine soft hairs; culms often densely branched above and reclining in the autumn phase; leaves strongly erect; primary panicle usually exserted from its sheath about the length of the panicle axis or less; leaves of winter rosette erect, with adaxial surfaces softly pubescent; plants from The Geysers, Sonoma Co., California . . . 3. var. *thermale*
   2. Plants variously pubescent, glabrate, or glabrous on the adaxial surfaces of the blades or nearly throughout, but not finely and softly pubescent; culms usually erect or ascending in the autumnal phase, not often heavily branched above and reclining; leaves ascending or spreading, rarely erect; primary panicle generally exserted from the sheath well over the length of the panicle axis; leaves of winter rosette mostly ascending or spreading, the adaxial surface glabrous; widespread . . . 1. var. *fasciculatum*

1. Dichanthelium lanuginosum (Ell.) Gould var. **fasciculatum** (Torr.) Spellenberg, comb. nov. — *Panicum dichotomum* L. var. *fasciculatum* Torr., Fl. North and Mid. U.S. 145. 1824. — *P. huachucae* var. *fasciculatum* (Torr.) Hubb., Rhodora 14:171. 1912 — *P. lindheimeri* var. *fasciculatum* (Torr.) Fernald, Rhodora 23:288. 1921. — *P. lanuginosum* var. *fasciculatum* (Torr.) Fernald, Rhodora 36:77. 1934. HOLOTYPE: "in sandy fields, New Jersey", said to be in the Columbia University Herbarium, now housed at NY, could not be located. Photograph of type, US.

Panicum dichotomum var. *pubescens* Munro ex Benth., nom. nud. Pl. Hartw. 341. 1857. Sacramento, Calif., *Hartweg 2024,* fragment at US!

Panicum huachucae Ashe, J. Elisha Mitchell Sci. Soc. 15:51. 1898 — *P. lanuginosum* var. *huachucae* (Ashe) Hitchc., Rhodora 8:208. 1906. HOLOTYPE: *Lemmon,* in 1882, "Huachucae Mts. Ariz.", US!

Panicum tennesseense Ashe, J. Elisha Mitchell Sci. Soc. 15:52. 1898. — *Panicum lanuginosum* var. *tennesseense* (Ashe) Gleason, Phytologia 4:21. 1952. HOLOTYPE: No. 7087 Biltmore Herbarium; Cedar Glades, La Vergne Co., Tennessee, 7 Aug 1897, not located; fragments and photograph of type at US!

Panicum occidentale Scribn., Annual Rep. Missouri Bot. Gard. 10:48. 1899. HOLOTYPE: *Haenke,* the locality as published by Presl in Reliquiae Haenkeanae "Hab. in Nootka-Sund", Vancouver Island,

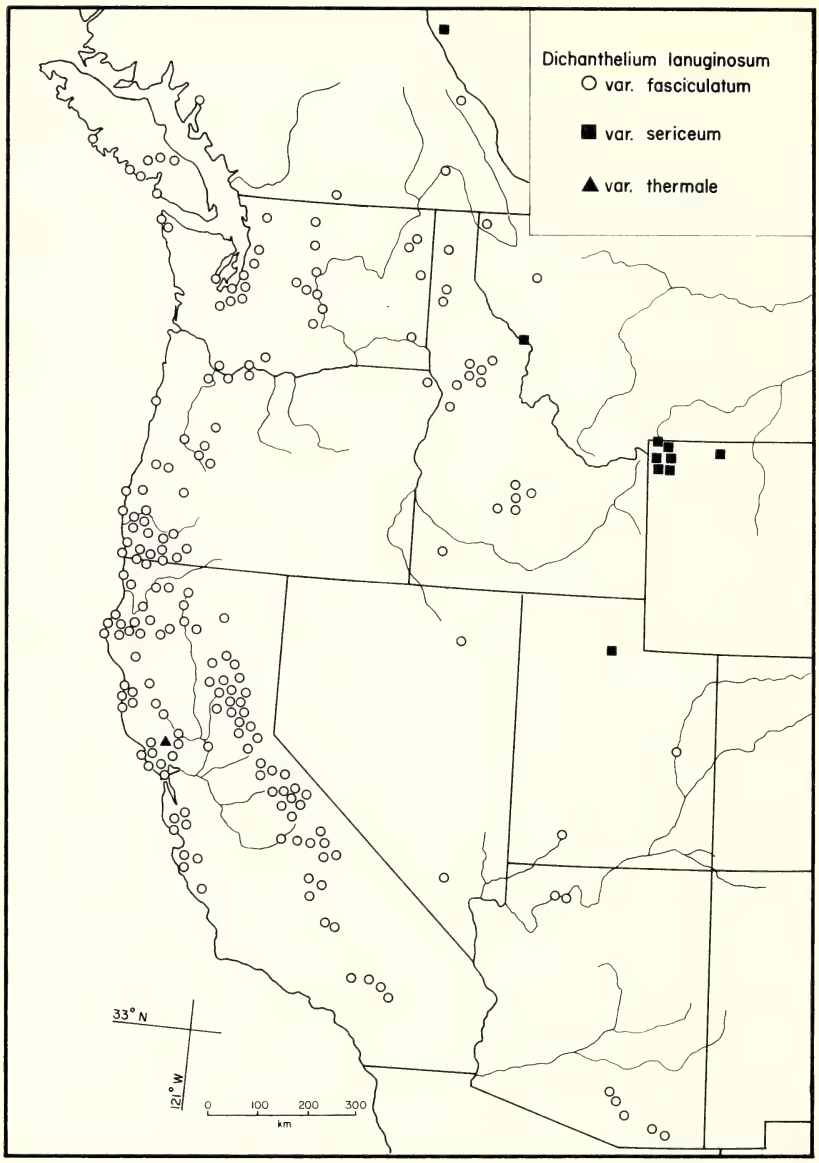

FIG. 4. Distribution of the varieties of *Dichanthelium lanuginosum* in western North America.

British Columbia, PR; photograph and fragments at US. ISOTYPE: The specimen Scribner saw when he named the species, but did not formally describe it, is believed to be in the Bernhardi Herbarium at MO; not located. PARATYPE: *A. A. & E. G. Heller 3978*, "collected near Montesano, Chehalis Co., Wash.", US! UC!

Panicum huachucae var. *silvicola* Hitchc. & Chase in Robinson, Rhodora 10:64. 1908. HOLOTYPE: *A. Chase 2400,* "Woods border, Reno, District of Columbia", US!

Panicum pacificum Hitchc. & Chase, Contr. U. S. Natl. Herb. 15:299. 1910. HOLOTYPE: *A. S. Hitchcock 3070,* Amer. Gr. Nat. Herb. no. 136, "in moist places in woods", Castle Crags, Shasta Co., Calif., US! ISOTYPES: CAS! UC! WTU!

Panicum brodiei St. John, Fl. Southeast. Wash. and Adj. Idaho, 51. 1937. HOLOTYPE: *D. A. Brodie,* Wawai, Snake River, Whitman Co., Wash., June 1893, WS! photograph UC!

Panicum lassenianum Schmoll, Madroño 5:95. 1939. HOLOTYPE: *W. L. Jepson 4082,* Devil's Kitchen, Hot Spring Valley, Plumas Co., Calif., US.

Diagnostic features: Leaves of winter rosette usually glabrous on the adaxial, and sometimes on the abaxial, surface; culms (5)30–60(80) cm tall, the autumnal form with branches short and tightly fascicled at the summit of the sheath or with longer and more loosely fascicled branches; sheaths of vernal leaves (2)3–6(8) cm long, about half the length of the internode; larger vernal blades linear-lanceolate to lanceolate (2.5)5–10(12) cm long, averaging more than 8.2 times as long as broad, pubescent, glabrate, or glabrous on the adaxial surface; primary panicles (3)4–9(13) cm long and about as wide; spikelets of the terminal panicles (1.5)1.6–2.0(2.1) mm long (averaging 1.65 mm east of the Rocky Mts., 1.8 mm westward); $2n = 18$. March through August.

Sandy lake margins, riverbanks, coastal slopes, marshy areas, moist to rather dry prairies from sea level to about 1370 m in Idaho and to 2120 m in the Sierra Nevada, southern British Columbia to Nova Scotia southward to southern California and the Gulf States; introduced in Japan (western distribution, fig. 4).

Dichanthelium lanuginosum var. *fasciculatum* is a widespread, variable assemblage of forms that includes no clearly separable entities. If the plants were generally pubescent they generally have been placed previously in *Panicum huachucae* when collected from Arizona eastward, or in *P. pacificum* if collected from California to British Columbia and Montana. Hitchcock and Chase stated that these two taxa resemble one another, but maintained that the spreading habit of *P. pacificum,* its larger spikelets, and its distinct range made it impossible to include it with the other. The spikelets of *P. huachucae* are 1.6–1.8 mm long, whereas those of *P. pacificum* are said to be 1.8–2.0 mm long, but numerous collections have spikelets shorter than this (fig. 1). *Panicum pacificum* is also said to have decumbent or prostrate-spreading autumnal culms, those of *P. huachucae* being stiffly erect or ascending. Most specimens of *P. pacificum* are collected too early in the season to indicate their autumnal form, but among those collected late in the season erect-

ascending forms are common. Most of my living collections have also had erect-ascending culms in the fall.

I have also included *P. lassenianum,* usually placed in *P. thermale,* in this variety. In describing the species, Schmoll (1939) noted its resemblance to *P. pacificum* of the Sierran region, although plants from the Mt. Lassen region tend to have slightly shorter leaves. Spikelets of the two are about the same length. Schmoll indicates the difficulty of separating the two by annotating as "*P. pacificum*-group?" the collection *J. Swallen 878* ("moist soil along creek close to hot sulphur springs. Trail to Lassen Peak", US). Such specimens as this and those of *T. H. Kearney,* Boiling Springs Lake, near Drakesbad, CAS; *J. T. Howell 35771,* Boiling Spring Lake, CAS; *H. N. Bolander 2169,* hot spring, southeast of Lassen's Peak, US; *R. Spellenberg 1229d,* Devil's Kitchen, WTU—all from the vicinity of Mt. Lassen, Calif.—are inseparable from more or less short, broad-leaved forms of *P. pacificum,* especially those from higher elevations in the Sierra Nevada. *Panicum lassenianum* is near the northern limit of these grasses in these mountains and may be part of a physiologically differentiated climatic and edaphic ecotype. However, I believe it is insufficiently distinct to be given formal taxonomic recognition.

When compared to var. *thermale* from The Geysers, the plants from the vicinity of Mt. Lassen are shorter (average culm length is 22 cm versus 40 cm), have shorter vernal blades, and have low winter rosettes of short, broad, more or less glabrous leaves. Though plants from these two areas are readily separable, those from Lassen are much more difficult to distinguish from some of those of var. *sericeum* from Yellowstone. Plants from the Lassen region have spikelets averaging 1.9 mm in length, 0.2 mm greater than the average of those of the var. *sericeum,* but spikelet lengths of plants of Lassen and Yellowstone completely intergrade. The leaves of the Lassen plants are slightly longer on the average but are not clearly different from those of the var. *sericeum.* Although the proportions of the leaves from the two populations overlap, the length/width ratio of those from Lassen averages about 8.4, whereas that of var. *sericeum* averages 6.5. As Schmoll noted, the abaxial blade surfaces of the Lassen plants are less densely pubescent than those of var. *sericeum* but this distinction is so subtle that it is of little diagnostic value.

Included in variety *fasciculatum* is *P. occidentale,* the western form with glabrate or glabrous adaxial surfaces of the blades. I earlier annotated such specimens as *P. lanuginosum* var. *tennesseense,* but such a separation is arbitrary and has no ecological, morphological, or geographic significance. The following collections are mixed, containing forms formerly referred to *P. pacificum* and *P. occidentale:*

J. B. Davy 5894, "among rocks, Martin's Ferry," Humboldt Co., Calif. (UC); *J. B. Davy and W. C. Blasedale 5971,* Crescent City, Del Norte Co., Calif. (UC 53350 = "*P. pacificum*", UC 39267 = "*P. occidentale*"),

J. T. Howell 381, along Merced River, Wawona, Mariposa Co., Calif., CAS; *P. H. Raven 4885,* hot springs, Blaney Meadows, Fresno Co., Calif., UC; *J. P. Tracy 5014,* boggy ground, White Thorn Valley, Humboldt Co., Calif., UC; *J. P. Tracy 9427,* along river, Trinity River Valley, at Willow Creek, Humboldt Co., Calif. (CAS = *P. occidentale*", UC = *P. pacificum*").

A number of collections have such short hairs or are so sparsely pubescent on the adaxial blade surfaces that they can be considered intermediate between forms formerly referred to *P. pacificum* and *P. occidentale.* A few of these are:
B. Bolt 503, Big Trees quadrangle, Tuolumne Co., Calif., UC; *J. B. Davy 6745,* Point Reyes Peninsula, Marin Co., Calif., UC; *A. Eastwood and J. T. Howell 3613,* Craft Lake, Coos Co., Ore., CAS; *J. A. Ewan 10482,* 5 mi S of Bandon, Coos Co., Ore., WTU; *J. B. Flett,* in 1897, prairie, Tacoma, Wash., WTU; *A. E. and E. G. Heller 3978,* near Montesano, Chehalis Co., Wash., UC; *F. L. Henderson,* in 1892, prairies of Pierce and Thurston Co's., Wash., WTU; *R. F. Hoover 2418,* Ione, Amador Co., Calif., UC; *R. F. Hoover 5140,* 5 mi NW of Santa Cruz on Empire Grade Rd., Santa Cruz Co., Calif., UC; *J. T. Howell 29842,* 1.5 mi NNE of Buena Vista, Amador Co., Calif., CAS.

Plants from about Point Reyes, California, to Nootka Sound, Vancouver Island, British Columbia, form a more or less recognizable coastal race distinguished by their tendency to be tightly tufted, the branch culms attaining about half the height of the vernal culms, the plants thus appearing leafy below. A plant with glabrous adaxial surfaces of the blades from this race was described as *P. occidentale.* In the interior, plants are commonly taller and more open and seemingly less leafy below. A robust plant of this form was described as *P. brodiei.* It is through these forms of the interior that typical *P. occidentale* grades into *P. tennesseense,* but some plants of the latter, especially in the Great Lakes region, have habits similar to that of the coastal race of the West.

Dichanthelium lanuginosum var. *fasciculatum* also intergrades with the southeastern var. *lanuginosum* through such lightly pubescent material as *S. M. Tracy 4508* (Biloxi, Miss., NY!, US, the type collection of *P. ciliosum,* a synonym of *P. lanuginosum,* sensu stricto) or such short-spikeleted, generally pubescent plants as *D. J. Banks 201* (roadside 1 mi SE of Boaz, Marshall Co., Ala., US) or *G. V. Nash* (vicinity of Lake Eustice, Lake Co., Fla., April 1–15, 1894, US). Numerous collections from eastern Texas are also intermediate between the two.

In two areas of the Northwest (including north coastal California where *P. occidentale* and *P. pacificum* are sympatric) plants that are subglabrous or glabrous are fairly common. These plants approach *P. lindheimeri,* a species distinguished by its elongate internodes, glabrous leaves and wiry culms, and small spikelets averaging about 1.5 mm long, widespread in the eastern half of the country but occurring sporadically

through the Southwest and into southern California as *P. funstonii* (*F. W. Coville and F. Funston 1286,* "on the banks of the Kaweah River, at Three Rivers, Tulare Co., Calif.", US!). Most of the plants from the Northwest that approach this species are more compact, have sparsely pubescent or puberulent sheaths, culms, or abaxial blade surfaces, and may in some have spikelets over 1.7 mm long. Since I am not very familiar with the Spreta group in the field, or the relationship between this group and the group Lanuginosa, I am hesitant to place these forms into *D. lindheimeri,* extending the range of that species 1600 km, or to place *D. lindheimeri* into *D. lanuginusum* as a variety, as Gleason (1952) and Fernald (1934) have done. Instead, I consider these plants to be representative of one of the extremes of variation in *D. lanuginosum* in the West. They are:
A. S. Hitchcock, Amer. Gr. Nat. Herb. no. 527, Eureka, Calif., UC; *A. R. Kruckeberg 2320,* Imnaha River, Wallowa Co., Ore., WTU, ORE, UC, OSC; *R. Spellenberg 1436,* Peshastin, and *1532,* Leavenworth, Chelan Co., Wash., WTU; *W. N. Suksdorf 5162,* and *5174,* Bingen, Klickitat Co., Wash., UC; *J. P. Tracy 925,* in wet ground at Eureka, Humboldt Co., Calif., (a mixed collection of glabrous and more or less pubescent plants), CAS; *J. P. Tracy 4645,* at Eureka, Humboldt Co., Calif., (a collection on which Tracy has noted "least pilose form" and is similar, except in pubescence, to his collection *4644,* on which he has noted "moderately pilose form") both at UC; *K. Whited,* in 1901, Tumwater Canyon, Chelan Co., Wash., WTU.

2. **Dichanthelium lanuginosum** var. **sericeum** (Schmoll) Spellenberg, comb. nov. — *Panicum ferventicola* var. *sericeum* Schmoll, Madroño 5:92. 1939. HOLOTYPE: *A. Nelson 6037,* Mammoth Hot Springs, Yellowstone National Park, Wyoming, RM. ISOTYPES: G, US!

Panicum ferventicola Schmoll, Madroño 5:92. 1939. HOLOTYPE: *A. Chase,* Amer. Gr. Natl. Herb. no. 137, 5 mi N of Norris Geyser Basin, Yellowstone National Park, Wyoming, G. ISOTYPES: UC! US! PARATYPES: *E. A. Mearns 4203,* "The Thumb, Yellowstone Lake", US! *A. S. Hitchcock 1902,* Norris Basin, around hot springs", US!

Panicum ferventicola var. *papillosum* Schmoll, Madroño 5:94. 1939. HOLOTYPE: *A. S. Hitchcock,* Amer. Gr. Natl. Herb. no. 220, Banff, Alberta, G. ISOTYPES: F, UC!

Diagnostic features: Plants low, tufted, densely pubescent (rarely subglabrous), sometimes forming dense mats; vernal culms (5)7–28(35) cm tall, stiffly erect-ascending to more or less spreading; branch culms attaining about half the height of the vernal culms, the plants thus appearing densely leafy below; sheaths often equaling or exceeding the

internodes, averaging 0.8–0.9 times their length, densely villous with ascending or spreading, often prominently papillate-based hairs; vernal blades ascending or spreading, rarely erect, (3)4–6(7.5) mm long, (5)6–10(14) mm wide, the length/width ratio averaging 6.5, the upper surface moderately to densely pubescent, rarely glabrous; primary panicles usually well exserted, (2.5)3–7(8) cm long and about as broad; spikelets (1.5)1.6–1.8(1.9) mm long; $2n = 18$. Mid-June through August.

About geysers, hot springs, and fumaroles, in gravelly, mineralized soil to heavy soil along warm creeks, usually in warm or hot ground, in the Rocky Mountains from about 1370 m at Banff, where probably extinct due to commercial development, south to Yellowstone National Park where it occurs at up to 2280 m, east to Buffalo Fork, Bighorn Co., Wyoming; reported from one collection from a garden in Salt Lake City, Utah (*W. A. Stanton, 826,* US) (fig. 4).

Variety *sericeum* is distinguished from the other varieties by its short culms, tightly clumped habit, and short, broad leaves. This tendency toward relatively broad leaves reaches its extreme in plants from Banff where the blade length is only about four times that of the width. The average length/width ratio rarely exceeds 8.0, serving to separate it from most of the plants of var. *fasciculatum* from nearby areas. Some plants from Lolo Hot Springs, Missoula Co., Montana, are low, tufted, and broad-leaved (*W. Griffiths 306,* US) and are readily placed in the var. *sericeum,* whereas others from the same springs (*R. Spellenberg 545,* WTU) have elongated culms and leaves slightly longer than 8.0 times their width, thus more closely resembling var. *fasciculatum.*

Other collections that on the basis of leaf proportions approach northern forms of *D. lanuginosum* var. *fasciculatum* are:
E. C. S. 319, Mammoth Hot Springs, US; *A. S. Hitchcock 2061,* Washburn Hot Springs, US; *A. S. Hitchcock 2086,* hot springs, 1 mi north of Thumb, US; *J. W. Lettermann,* in 1885, Hayden's Valley, US; all from Yellowstone, and *R. Spellenberg 523,* Huckleberry Hot Springs, Teton Co., Wyo., WTU.

3. **Dichanthelium lanuginosum** var. **thermale** (Boland.) Spellenberg stat. et comb. nov. — *Panicum thermale* Boland., Proc. Calif. Acad. Sci. 2:181. 1862. HOLOTYPE: *H. N. Bolander 3941,* The Geysers, Sonoma Co., Calif., G. ISOTYPES: US! UC! CAS!

Diagnostic features: Plants forming large tufts, (30)35–50(60) cm tall, densely and softly pubescent throughout, or occasionally only sparsely pubescent on the abaxial surfaces of the blades; winter rosette of erect culms and leaves ⅕–¼ the height of the vernal culms, densely pubescent; sheaths (2.5)3–4(5) cm long, averaging about half the length of the internodes; vernal blades erect, (7)8–11(13) cm long, (5)6–8(10) mm wide, the blade length/width ratio usually over 10 and averaging 13.6, panicles usually exserted from the sheath only about the length of the

panicle axis or less, (4)5–9(11) cm long, about as wide; spikelets (1.7)1.8–2.0(2.1) mm long, averaging 1.9 mm: $2n = 18$. April to mid-August.

In mineralized, usually moist, warm "soil", at The Geysers, Sonoma Co., Calif. (fig. 4). The long standing record for Napa Co., based on *Brewer 861* (US), is probably in error. This specimen has two labels: one reads "At McDonald's Napa County" and the other reads "growing around all the Geysers Napa Co.". Correspondence with the Sonoma County Recorders Office has disclosed that a McDonald owned the property around The Geysers, Sonoma Co., in 1897, and probably before. I have seen no collections of *Dichanthelium* from hot springs in Napa Co.

This variety includes one of the most distinct forms of *Dichanthelium* from the West. Variety *thermale* is outwardly most similar to plants of var. *lanuginosum* from the Gulf Coastal Plain. They have similar habits late in season, the form of the fascicled branches of the two is sometimes similar, and both are densely and softly pubescent. In general, var. *thermale* has leaves longer relative to their width (length/width ratio averaging 13.6), slightly larger spikelets, less spreading leaves on the branch culms, and no cilia on the margins in the upper half of the leaves of the aestival foliage. The few collections of var. *fasciculatum* from Sonoma and Napa counties somewhat resemble var. *thermale* especially in leaf habit and leaf proportions: *J. T. Howell 13032,* Pitkin Marsh, Sonoma Co., Calif. (CAS) and *J. T. Howell 18240,* hills SW of St. Helena, Napa Co., Calif. (CAS).

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RELATIONSHIPS OF HESPEROLINON AND LINUM (LINACEAE)

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Hesperolinon is a genus of about a dozen closely related annuals, restricted mainly to serpentine soils of the North and South Coast Ranges of California. It was at first treated as a section of *Linum* (Gray, 1865) and later elevated to a genus (Small, 1907), a status upheld by Sharsmith (1961) who described *Hesperolinon* in some detail. At the same time, it is clearly related to *Linum* and its narrow geographical and ecological range, little morphological diversity, and rather high degree of specialization when compared to the large, diverse, and worldwide *Linum* suggest that *Hesperolinon* may be an evolutionary segregate of that genus.

A comparison of *Hesperolinon* with various species of *Linum,* as well as with other genera, reveals that it is among species of *Linum* sect. *Linastrum* that the most similar species are found. Sharsmith (1961, p. 273), after comparing *Hesperolinon* with species of several sections of *Linum,* concluded that "*Linum,* section *Cathartolinum* [*Linastrum*] (North American species only), in many ways bridges the morphological hiatus between the rest of *Linum* and *Hesperolinon.* There appears to be a stabilization in *Hesperolinon* of many of the tendencies found incipiently in *Linum* section *Cathartolinum* [*Linastrum*]."

A survey of the relationships of the approximately forty North American taxa of sect. *Linastrum* (Rogers, 1963, 1968, 1969) showed that they comprise five distinct "complexes". Some conclusions were also reached with regard to which species are primitive and which are specialized for several variable features in these North American species. A number of the characteristics that distinguish *Hesperolinon* from *Linum* appear to be further specializations of these. When these features and their distribution among the five complexes are compared with those possessed by *Hesperolinon,* it is possible to place these groups in a tentative evolutionary arrangement (fig. 1). Brief descriptions of these characters will help clarify how each has helped in interpreting relationships.

Staminodia. Diminutive structures alternating with the stamens have generally been interpreted as staminodia. They are found more or less throughout *Linum* and their absence is considered a specialization. In North American sect. *Linastrum* they are found only in the primitive *L. schiedeanum* complex. They are also absent in *Hesperolinon.*

Leaf arrangement. It was concluded (Rogers, 1969), on the basis of its close correlation with other features considered primitive among North American species of sect. *Linastrum,* that whorled basal leaves are primitive in this group. Evolution to opposite and alternate leaves has probably taken place several separate times and most of the North American species have opposite or alternate leaves. Only in the *L. schiedeanum* complex and in *Hesperolinon* are leaves in whorls.

Stipular glands. These structures are widespread in *Linum* and are uniformly present among North American species thought to be primitive. Their loss has clearly occurred in other sections of the genus as it has in the *L. virginianum* and *L. neomexicanum* complexes and a few species of the *L. rigidum* complex of sect. *Linastrum. Hesperolinon* species have retained this "primitive" character although the glands are commonly poorly developed.

False septa. The intrusion of false septa makes the fruit of *Linum* more or less ten-celled. Partially developed false septa are characteristic of most of the genus. Most of the *L. rigidum* complex and two or three species in the *L. virginianum* complex have complete or essentially complete false septa and are considered specialized with respect to this character. *Hesperolinon* is similar to other species of *Linum* in having incomplete false septa.

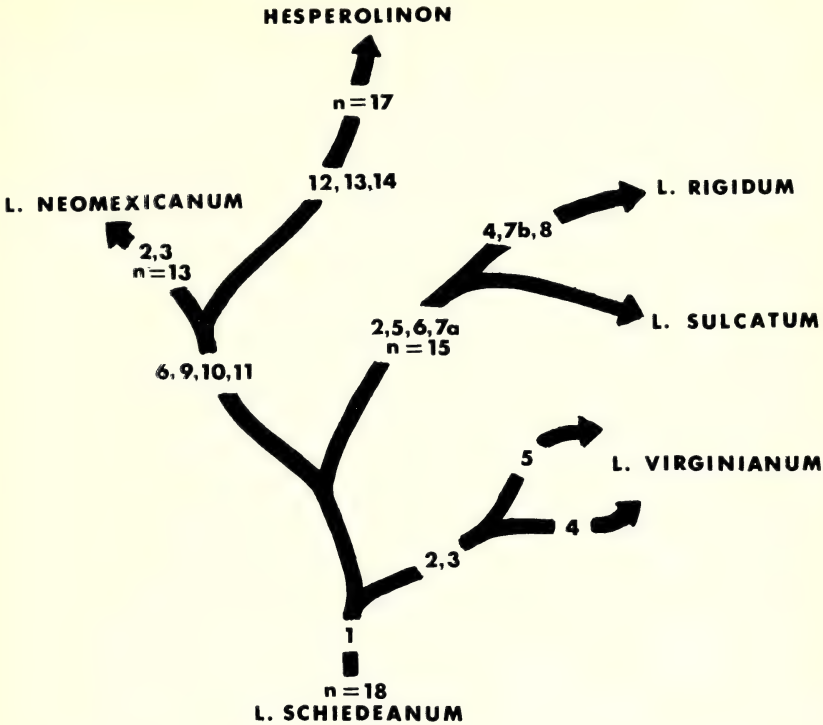

FIG. 1. Evolutionary relationships of five "complexes" of North American species of *Linum* sect. *Linastrum* and *Hesperolinon*. Changes in chromosome number are indicated; other numbers refer to the following: 1, loss of staminodia; 2, whorled → opposite or alternate leaves; 3, loss of stipular glands; 4, partially developed → completely developed false septa; 5, tricolpate → multiporate pollen; 6, perennial → some or all annual; 7a, separate → basally united styles; 7b, styles completely united or nearly so; 8, twice as many → same number of fruit segments as carpels; 9, acquisition of petal auricles; 10, acquisition of non-yellow corollas; 11, petal attachment at or near base → summit of stamen tube; 12, acquisition of conspicuous petal appendages; 13, five → three/two carpels and styles; 14, lens-shaped → wedge-shaped seeds in cross-section.

POLLEN MORPHOLOGY. The "basic" pollen grain in *Linum* is tricolpate, although multiporate pollen has evolved several times in the genus (Rogers and Xavier, 1972), including the *L. sulcatum* and *L. rigidum* complexes and some species of the *L. virginianum* complex. *Hesperolinon* has retained tricolpate pollen. Xavier (1967, p. 32) noted, "The pollen of the genus *Hesperolinon* resembles that of some species of the *Pringlei-neomexicanum* group and to the *Digynum* type. Similarity in pollen morphology and closeness of geographic distribution support the relationship between the *Pringlei-neomexicanum* group, *Digynum* and the *Hesperolinon* group."

Longevity. Almost all species of *Linum* are herbaceous. Perennials are generally considered more primitive than annuals. Annual species are found scattered throughout the genus. A number of North American species, principally the *L. sulcatum* and *L. rigidum* complexes, plus *L. neomexicanum* are annuals. All species of *Hesperolinon* are also annuals, although their comparative diminutiveness and delicateness tend to distinguish them qualitatively from *Linum*.

Union of styles. The five styles in *Linum* are usually separate. *Linum sulcatum* has partially united styles, while species of the *L. rigidum* complex are characterized by styles united nearly to the summit. *Hesperolinon* resembles more primitive species in having separate styles.

Fruit dehiscence. Fruit of *Linum* and *Hesperolinon* separate into twice as many one-seeded segments as carpels, except fruits of the *L. rigidum* complex, which are unique in the genus in splitting loculicidally into five two-seeded segments.

Petal auricles. Auricles at the base of the petals are generally present in *Hesperolinon* and have been cited as one of the generic characters. As Sharsmith noted, however, these are equally prominent in a few species of *Linum*. These prove to be the taxa that comprise the *L. neomexicanum* complex.

Petal pigmentation. With the exception of the white-flowered *L. pringlei* of the *L. neomexicanum* complex, sect. *Linastrum* is characterized by yellow flowers. *Hesperolinon* is about equally divided between white- and yellow-flowered species. A comparison of floral pigments among North American species of sect. *Linastrum* proved to be of considerable value in assessing relationships (Giannasi and Rogers, 1970). Giannasi has made some initial studies of the floral pigments of *Hesperolinon* and makes the following statement (pers. comm.): "a number of compounds found in *Hesperolinon* may also be observed in *Linum:* specifically in the *L. schiedeanum* and *L. neomexicanum* taxa, rather than the *L. rigidum* taxa." Apigenin-c-glycoside, characteristic of all five of the *Hesperolinon* species tested (including both white- and yellow-flowered species), was found otherwise only in species of the *L. neomexicanum* complex.

Petal attachment. One of the features that Sharsmith (1961) stressed as helping to set *Hesperolinon* apart from *Linum* is the attachment point of the petals, which in *Hesperolinon* is at the summit of the stamen tube in the usual position of the staminodia. In most species of *Linum* they are attached at or near the base of the stamen tube. It is very likely significant, therefore, that the few exceptional species of *Linum* that have petals in this unusual position are those of the *L. neomexicanum* complex.

Petal appendages. These consist of "horizontal crests" located near the auricles and a central appendage on the midvein near the base of the petal. These are commonly well developed in *Hesperolinon* and served as the principal feature upon which Small (1907) removed these species

from *Linum*. They are apparently present, although less developed, in *Linum* as well. Sharsmith (1961) mentioned species of the *L. rigidum* and *L. neomexicanum* complexes particularly, so although their prominence in *Hesperolinon* is a reasonable generic character, they seem to be best interpreted as a further elaboration of structures already present in species of sect. *Linastrum,* to some extent even among the species considered primitive.

Style and carpel number. The entire genus *Linum* is characterized by five-carpellate fruits. Perhaps the most significant constant difference between *Linum* and *Hesperolinon* is that the latter has three- or two-carpellate fruits.

Seed shape. Seeds of *Linum* are uniformly lens-shaped in cross-section, while those of *Hesperolinon* are narrowly triangular or wedge-shaped in cross-section. Seed shape is correlated with and may in fact be an effect of the reduced carpel number but does constitute an additional generic difference. *Sclerolinon digynum,* another species of far western United States, also has wedge-shaped seeds in two carpellate fruits. It is surely related to both *Hesperolinon* and *Linum,* although many basic dissimilarities preclude its being on a direct evolutionary line involving *Linum* and *Hesperolinon* (Rogers, 1966).

Chromosome number. Chromosome numbers have been established for most of the North American taxa of *Linum* and *Hesperolinon.* The primitive number in the North American species of the sect. *Linastrum* appears to be $n = 18$ (Harris, 1968). It is characteristic of the *L. schiedeanum* and *L. virginianum* complexes, while the *L. sulcatum* and *L. rigidum* complexes, with $n = 15$, and the *L. neomexicanum,* with $n = 13$, are thought to be aneuploid derivatives. Of the eleven species of *Hesperolinon* for which chromosome numbers are known, seven have $n = 18$ and four have $n = 17$. The lower number is to a degree correlated with reduction of carpel number from three to two (Rogers et al., 1972).

Geographical Distribution. Although it is clear that distributions at the time the diversification into *Hesperolinon* and the various complexes of *Linum* was taking place may have been quite different from the present ones, the close resemblance of *Hesperolinon* to North American species rather than to those of other parts of the world is significant. Within the North American sect. *Linastrum,* the *L. rigidum* and *L. neomexicanum* complexes are geographically nearest to *Hesperolinon,* although none overlaps the range of *Hesperolinon.*

Conclusions

On the basis of interpretations presented here, it is possible to draw conclusions about evolutionary relationships among North American complexes of *Linum* sect. *Linastrum* and *Hesperolinon.* Species of the *L. schiedeanum* complex, as noted earlier, are thought to possess the greatest number of primitive features. The *L. virginianum, L. sulcatum, L. rigidum,* and *L. neomexicanum* complexes each have traits that set

them apart from a possible evolutionary line leading from *L. schiedeanum* to *Hesperolinon*. The *L. virginianum* complex, although differing from species of the *L. schiedeanum* complex in only a few characteristics, is best interpreted as constituting a small evolutionary side branch of closely related eastern North American species. The *L. sulcatum* and *L. rigidum* complexes, because of their similarity in chromosome number, united styles, and unique multiporate pollen, are thought to constitute another line of evolution, culminating in some of the most highly specialized species in the genus. While the *L. neomexicanum* complex is also a specialized group with a unique chromosome complement, most of the features that make it unique in *Linum* are ones in which it resembles *Hesperolinon*. *Hesperolinon* can be described as having a combination of the primitive features found in the *L. schiedeanum* complex and of traits found in the *L. neomexicanum* complex. Excluding the few generic traits unique to it, *Hesperolinon* possesses no features that are not found in the *L. schiedeanum* or *L. neomexicanum* complex or both.

Postulated relationships are shown in Figure 1. The hypothetical "common ancestor" to *Linum* and *Hesperolinon,* located at the juncture at which *L. neomexicanum* branches off the line leading from *L. schiedeanum* to *Hesperolinon,* would be characterized by features retained from its *L. schiedeanum* ancestor (whorled leaves, stipular glands, partially developed false septa, tricolpate pollen, separate styles, dehiscence of fruit into twice as many segments as carpels, seeds lens-shaped in cross-section, and chromosome number of $n = 18$), together with features that *L. neomexicanum* shares (absence of staminodia, annual habit, presence of petal auricles, white as well as yellow flowers, and petals attached at the summit of the stamen tube). The reduction of carpel number and concomitant alteration of seed shape and the elaboration of petal appendages are the principal morphological features that set *Hesperolinon* apart from this common ancestor. Its geographical and ecological isolation from closely related species may also be significant. *Hesperolinon* is clearly not separated from *Linum* by a great array of characters. There is, however, a distinct gap between it and species of the *L. neomexicanum* complex, which appears to include its nearest relatives.

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Distributional and Ecological Notes on Pinus culminicola.—Until recently, Potosí piñon or *pino enano* in Spanish vernacular, *Pinus culminicola* Andresen & Beaman, a high altitude dwarf piñon, was known only from the summit of Cerro Potosí (ca 3600 m) in Nuevo León (24° 53′ 30″ N, 100° 10′ 30″ W) where it was thought to be endemic (Andresen and Beaman, J. Arnold Arbor. 42:437–441, 1961; Beaman and Andresen, Amer. Midl. Naturalist 75:1–33, 1966). However, in 1972, Capó-Arteaga in an unpublished thesis (*Observaciones sobre la taxonomia y distribución de las coníferas de Nuevo León, Mexico.* Tesis, Fac. Ciencias Biol., Univ. Nuevo León, Monterrey, N.L.) and again in a popular Mexican forestry journal (Bosques 9:33, 1972) mentions that he collected the Potosí piñon from the Sierra de la Marta in Nuevo León; no additional information was presented.

Recent collections that substantiate the distribution for *Pinus culminicola* are cited below: Mexico, Coahuila, Mcpo. Arteaga, Sierra de Santa Maria E and S of La Ciruela, 12 Feb 1974, *Patterson 1102* (TEX); Sierra San Antonio, 5 km N of San Antonio de las Alazanas, 8 Oct 1974, *Patterson 32, 33* (TEX); head of Cañon San Antonio de las Alazanas between Sierra San Antonio and Sierra San Antonio de las Alazanas 7.5 km ENE of San Antonio de las Alazanas, 9 Oct 1974, *Patterson 36* (TEX). Nuevo León, Mcpo. Rayones, Sierra de la Marta, 21 Aug 1970, *Capó-Arteaga and Villarreal C. s.n.* (UNL).

The Coahuila-Nuevo León boundary falls along the Sierra de la Marta (also known as S. Santa Marta) axis but Mexican maps vary considerably in the placement of the state boundary. Both the Sierra de la Marta and the Sierra de San Antonio reach elevations in excess of 3400 m and are of a dolomitic limestone bedrock (at least in the upper portions). In addition, both sierras trend east-west and have extensive sheltered north exposures that rise steeply from a 2400 m base elevation. Sierra de la Marta is approximately 25° 13′ N, 100° 23′ W; Sierra San Antonio is 25° 17′ N, 100° 38′ W (fig. 1).

All of the Potosí piñon that we observed is restricted to open rocky sites at high elevations (above 3000 m) in sheltered sites usually but not exclusively on northern exposures. Such sites as the open summits of scarp faces or along high altitude crests of sierras seem to be preferred, e.g., on the Sierra de la Marta. We have also observed *P. culminicola* on shallow rocky soils in open sites within a mixed-conifer forest (S. de la Marta) as well as on open, rocky sites in mixed-conifer parklands (S. de San Antonio). In addition, *P. culminicola* is peripherally associated with an aspect of a high elevation (3000 m +) depauperate, open montane chaparral (sensu Muller, Amer. Midl. Naturalist 21:701–703, 1938) with low, gnarled, deciduous and evergreen scrub oaks, a variety of rosaceous and rhamnaceous shrubs and an *Agave* as the dominant associates (see *Patterson 36*).

In favorable habitats on the Sierra de la Marta, *P. culminicola* is frequently associated with a *Pinus-Pseudotsuga-Abies* community whose dominant species include *Pinus hartwegii, Pinus strobiformis, Pseudotsuga flahaultii,* and *Abies vejarii* (includ-

FIG. 1. Distribution of *Pinus culminicola*.

ing var. *macrocarpa*). At the upper limits of the S. de la Marta (3400 m +), *P. culminicola* is more frequently associated with *Picea mexicana* and at the summit of the ridge Potosi piñon grows inclose proximity to a montane chaparral community that dominates the southern slope of the S. de la Marta. *Pinus culminicola* associates either with a *Pinus hartwegii* parkland community or with a *Pinus-Pseudotsuga-Abies* community on favorable sites in the Sierra de San Antonio at elevations in excess of 3200 m.

Although *P. culminicola* was fairly common at each of our collecting sites, we did not observe a well-developed, extensive *P. culminicola* scrub community as described by Beaman and Andresen (Amer. Midl. Naturalist 75:8, 18, 1966) for Cerro Potosí. However, on the northern exposure just below the ridgeline of the S. de la Marta there occurs a relatively homogeneous but discontinuous *P. culminicola* community of perhaps 10 m in width.

We have no evidence to support Beaman and Andresen's (op. cit.: 18, 20) contention that *P. culminicola* is a timberline or subalpine species. There is no indication of a timberline on either S. de la Marta or S. de San Antonio. We observed that *P. culminicola* was most commonly associated with those species that Beaman and Andresen (ibid.: 22) described as occasional associates of the *Pinus hartwegii* forest community at lower elevations on Cerro Potosí. Such an occurrence is no doubt explained by the limited available habitat, with the resultant telescoping of plant communities, on the S. de la Marta and the S. San Antonio, since as Beaman and Andresen (op. cit.) observed, the *P. culminicola* scrub community does merge with the *P. hartwegii* forest community at about 3300–3500 m on Cerro Potosí. Unfortunately, there is a paucity of accurate elevation determinations for most of the sierras of northeastern Mexico and such a handicap makes meaningful comparisons

of elevational range of taxa or indeed communities extremely tenuous. That *P. culminicola* grows in association with an open montane chaparral seems to contraindicate that Potosí piñon is strictly a timberline or subalpine species.

Although we have no quantitative supportive data, *P. culminicola* appears to be a typical ecotonal species, at least in the area that we examined. Potosí piñon appears to colonize (1) the edge between the upper environmental limits of the mixed conifer community and the crest of the Sierra de la Marta, (2) an environmental edge above steep scarp faces on lower (3000 +) northern exposed slopes of the Sierra de la Marta, (3) environmental or edaphic edges (or ecotones) between mixed conifer forests or parklands and other formations such as montane chaparral at high elevations of 3000 m +, and (4) openings at high elevations on sheltered slopes in the mixed conifer forest community usually caused by variation in substratum, i.e., locally rocky sites with thin soils.

The patchy, seemingly unpredictable distribution of the Potosí piñon is not easily understood. Peña Nevada, ca 3400 m, approximately 140 km south of Cerro Potosí (see fig. 1) and approximately 200 m lower in elevation has been surveyed by the authors and does not have *P. culminicola* as a component of its florula (see also Beaman and Andresen, op. cit.: 31).

Nomenclature for *Pinus* is based upon Critchfield and Little (op. cit.); nomenclature for other conifers mentioned in the text is based upon Martinez (*Las Pinaceas Mexicanas,* 3rd ed. Univ. Nac. Autón. de México, 1963). Place names and approximate elevations are based upon the Army Map Service (AMS), Edition 1, 1:250,000, Monterrey Sheet, NG14–7, 1962.

The authors gratefully acknowledge the assistance of the following individuals: Debbie Balser for typing the manuscript; Fernando Chiang, Marshall C. Johnston, Raymond Neck, and Judy Riskind for their editorial assistance; Jorge Marroquín for calling out attention to the pertinent Mexican references on the Potosí piñon; and to Barry Wagner for drafting the figure.—David H. Riskind and Thomas F. Patterson, Resource Management Section, Texas Parks and Wildlife Department, John H. Reagan Bldg., Austin, Texas 78701.

Bacopa monnieri (Scrophulariaceae), a New Record for California.—A small but well-established population of *Bacopa monnieri* (L.) Wettst. has been discovered: California, Riverside Co., ca 11 km (6.5 mi) SE of Vidal, damp soil on shore of Colorado River at Agnes Wilson Rd., 16 Nov 1974, *Gordon et al. 775* (RSA). This semi-aquatic is widespread in tropical regions throughout the world. In North America it occurs in Texas, thence east to Florida and north to Virginia (Correll and Johnston, *Manual of the vascular plants of Texas,* 1970), and, in western Mexico north to the Sonoran Desert of central Sonora and southern Baja California (Shreve and Wiggins, *Vegetation and flora of the Sonoran Desert,* 1964).

Plants in the new population are locally abundant, forming small mounds among other river-bottom herbs, notably *Aster exilis* Ell., *Eustoma exaltatum* (L.) Griseb., and *Eleocharis coloradoensis* (Britt.) Gilly. The population has existed at the Wilson Road site for at least 5 years; it was first noted on 15 Nov 1969, when it appeared to be at least as firmly entrenched as it is today.

Kearney and Peebles (*Arizona flora,* 1960) reported a 1912 collection by *Pinney* (ARIZ) identified as *Bacopa eisenii* (Kell.) Penn. from the Gila River between Phoenix and Maricopa, Maricopa County, Arizona, approximately 250 km (155 mi) ESE of the Wilson Road site. We have examined these sheets and concur in the identification. Assuming the Arizona colony is still extant, it would represent the closest population of *Bacopa,* geographically, to the Wilson Road population.—Michael H. Grayum and Kenneth A. Wilson, Biology, California State University, Northridge 91324.

New Plant Records for California.—Several species previously unrecorded for Fresno County, California, were collected in the spring of 1974 on and around Table Mountain. Subsequent work at the herbarium of California State University, Fresno, Jepson Herbarium, California Academy of Sciences, and University of California, Berkeley, revealed a number of plants either improperly identified or not previously recorded. Notes on these plants, representing native and naturalized species, are included here. While naturalized species may be recent introductions, it is thought that those native to California have gone undetected due to the inaccessibility of Table Mountain and lack of botanical interest in the area. Voucher specimens were placed in JEPS and, whenever possible, FSC herbarium.

The following six species, when collected in Fresno County and not specified otherwise, were found 7.5 km west by air from Prather, on the northwest corner of Table Mountain overlooking Temperance Flat at 600 m:

Downingia bicornuta Gray var. *bicornuta*. Fresno County: *Haines 74197*. Madera County: Kennedy Table at 742 m, *Silvernale,* 14 Apr 1961 (JEPS). These plants grew in heavy basaltic clay at the margin of large vernal pools at both sites. Merced County: Ryer, *Hoover 2092,* 6 May 1937(UC). This variety was formerly thought to have a southern limit of distribution in Stanislaus County (Munz, *A California flora,* 1959).

Parvisedum pumilum (Benth.) Clausen. Fresno County: *Haines 74075*. These plants, growing in close association with *P. Congdonii* (Eastw.) Clausen, were scattered over much of the rocky mountain top forming dense masses in shallow depressions. Stony Flat near Cedarbrook, *Hoover 4389,* 11 May 1940(UC). Madera County: Kennedy Table at 742 m, *Silvernale,* 14 Apr 1961(FSC). The previously recorded range for this species in the Sierra foothills was Merced County to Sutter County (Munz, op. cit.).

Streptanthus tortuosus Kell. var. *suffrutescens* (Greene) Jeps. Fresno County: *Haines 74084, Bitters 69103,* 9 Apr 1969(FSC). These plants were collected on sheer basaltic cliff faces. Mendocino County: 9.7 km south of Bell Springs on serpentine cliffs at 1198 m, *Ripley & Barneby 6835,* 16 Jun 1945(CAS). This perennial variety has been reported from similar habitats in Sonoma and Butte Counties (Munz, op. cit.).

Navarretia tagetina Greene. Fresno County: *Haines 74200, Weiler 65033,* 14 May 1965(FSC), *Bitters 69165,* 9 Apr 1969(FSC). Plants were from an extensive population growing in thin basaltic soil. Merced County: 8.9 km NNE of Schilling, *Belshaw,* 30 Apr 1936(UC). Tuolumne County: Chinese Camp, *Hoover 2370,* 3 Jun 1937(JEPS); Yosemite Junction, *Mason 11104,* 5 May 1936(UC). This species has been reported as bordering the Sacramento Valley and in the Sierra Nevada from Amador County north (Munz, op. cit.).

Brodiaea terrestris Kell. ssp. *kernensis* (Hoov.) Niehaus. Fresno County: *Haines 74201*. Plants were abundant in very thin basaltic clay overlying solid basalt. Madera County: near Iron Creek, *Raven 3799,* 6 Aug 1951(CAS). This species has a known distribution from Tulare and San Benito Counties south (Niehaus, 1971, Univ. Calif. Publ. Bot., vol. 60).

Trifolium dichotomum H. & A. Fresno County: *Haines 74197*; 9.5 km southwest by air from Prather, on the extreme west end of Table Mountain at 240 m, *Partridge 42,* 22 Mar 1974(FSC). Tulare County: between Richgrove and Ducor, *Hoover 470,* 30 Mar 1935(UC). Madera County: San Joaquin Experimental Range at 369 m, *Biswell 175,* 21 Apr 1938(UC). Stanislaus County: 3.2 km west of Patterson, *Hoover 4287,* 31 Mar 1940(UC). Calaveras County: Calaveras Valley, *Brandegee,* 18 Aug 1942(UC). This species was previously known from San Luis Obispo County to Humboldt County (Munz, *Supplement to a California flora,* 1968).

The following two species were collected in Fresno County, 5 km west by air from Prather, on Wellbarn Road below Table Mountain at 400 m:

Plagiobothrys distantiflorus (Piper) Jtn. Fresno County: *Haines 74082, Bitters 69033*(FSC); 16 km by air from Prather, on Italian Bar Road in Jose Basin at

600 m, *Haines 74094;* United States Forest Service engineer's camp, Haslett Basin at 568 m, *Haines & Evans C-75060,* 16 Mar 1975(FSC); 1.6 km on USFS road 10S02 from the junction with 10S69 in Haslett Basin at 737 m, *Haines & Evans C-75099,* 25 Mar 1975(FSC); USFS road 10S69, 4.5 km east of 10S02 at 870 m, *Haines & Evans C-75081,* 24 Mar 1975(FSC); USFS road 10S69, 8.7 km east of 10S02 at 1020 m, *Haines & Evans C-75079,* 24 Mar 1975(CSUF). All of these populations were present in moist seepages and vernal pool edges. Another population from Maxon Road near the Trimmer Ranger Station, *Weiler 67030,* 3 Apr 1967 (FSC), has not been relocated in subsequent years following road repair work in the area. These populations represent a southern extension of this rare and endangered California species (Powell, *Inventory of rare and endangered vascular plants of California,* 1974), previously known from Madera County to Tuolumne County (Munz, op. cit.).

Geranium molle L. Fresno County: *Haines 74096.* This extensive population formed a continuous mass following ephemeral streams. Sycamore Creek above Pine Flat Reservoir at 300 m, *Haines 74068*; Wonder Valley at 213 m, *Otto 67–134,* 5 May 1967(FSC); Burrough North Road at 600 m, *Robinson,* 31 Mar 1974(FSC). Inyo County: Independence, *Kerr,* 23 Jun 1941(CAS). This European native was previously recorded from the coastal parts of the state (Munz, op. cit., 1959).

Bromus sterilis L. Fresno County: 6 km west by air from Prather, on the northeast corner of Table Mountain overlooking Temperance Flat at 560 m, *Haines 74202.* The area had burned the previous summer and spring growth of annual herbs was vigorous, so that these plants could not be mistaken as depauperate *Bromus diandrus* Roth., which is closely allied in Munz's flora. *Bromus sterilis,* previously noted from Del Norte and Humboldt Counties, occasional further south (Munz, op. cit., 1959) and Monterey County (Munz, op. cit., 1968), seems to have a far broader distribution in California, with collections from Yolo(CAS), Alameda (JEPS), Stanislaus(JEPS), Santa Cruz(JEPS), San Luis Obispo(CAS, UC), Los Angeles(CAS), Calaveras(CAS), Tuolumne(CAS), Mariposa(CAS, UC), and Fresno (JEPS) counties.

Orthocarpus pusillus Benth. Fresno County: 16 km by air from Prather, on the Italian Bar Road in Jose Basin at 600 m, *Haines 74093.* Santa Barbara County: Point Sol, *Smith 2997,* 15 Apr 1951(CAS). Mariposa County: cut-off road from Mount Bullion to State Highway 140, 3.2 km south of Mount Bullion at 676 m, *Bacigalupi 4919,* 15 Apr 1955(JEPS). The previous range for this species was Coast Ranges from San Luis Obispo County north; occasional from Stanislaus County to Butte County (Munz, op. cit., 1959).—Robert D. Haines, Department of Biological Sciences, California State University, Fresno 93740.

The Ynés Mexía Collections and N. Floy (Mrs. H. P.) Bracelin.—Except for the dedicated and meticulous assistance of Mrs. Bracelin, the extensive Mexican and South American collections made by Ynés Mexía might never have been distributed. Once her beautifully prepared and carefully documented specimens reached home base, Mrs. Mexía had little interest in them other than the excitement and satisfaction of having obtained species new to science. Mrs. Bracelin said, "She [Mrs. Mexía] loved to have a trip and to see things and do things, but there had to be a purpose behind it." Mrs. Mexía and Mrs. Bracelin became friends in 1927 when they were both enrolled in Dr. Harold Bryant's "Six Trips Afield", a University of California Extension course. At that time Mrs. Mexía had made two collecting trips to Mexico and from the second one in 1926 [cf. Madroño 1:227–238. 1929]

she had brought back extensive collections that were still not completely processed. In January, 1928, "Bracie", as she was known to friends, took over the processing of the Mexican and subsequent South American collections—preparing labels, sending sets to specialists for naming, arranging sales, and, finally, distributing the duplicates. In this connection, Mrs. Bracelin built up a wide correspondence and acquaintanceship with botanists throughout the world. Before her death, Mrs. Bracelin deposited all of the records of the Mexía collections, much of the Mexía correspondence, and information about the Mexía family in the Bancroft Library, University of California, Berkeley. The first set of the Mexía collections is deposited in UC. Mrs. Bracelin published the following articles treating Ynés Mexía and her collections:

Bracelin, Mrs. H. P. Itinerary of Ynés Mexía in South America. Madroño 3:174–175. 1935.

———. Ynés Mexía. Madroño 4:273–275. 1938.

Inasmuch as Mrs. Mexía had arranged to bring her Mexican collections to the University of California Herbarium at Berkeley, Mrs. Bracelin worked on them there. In May, 1929, Dr. E. B. Copeland, who was at that time Curator of the Herbarium, employed Mrs. Bracelin as an Herbarium assistant. In the early 1930's Bracie helped Dr. Carleton R. Ball in working up his willow collections for the revision of the genus *Salix* in the western United States. Later, she set herself the task of making a collection of the exotic plants growing in the Anson and Anita Blake estate (now the property of the University of California, Berkeley). With duplicates, her 1392 garden collections amounted to about 20,000 sheets, all of which were distributed to herbaria expressing an interest in cultivated plants. After leaving the University of California Herbarium, she perfected her skills as a scientific illustrator (specializing in the field of graphs and charts). From January, 1940, to July, 1943, Mrs. Bracelin was an assistant in the Botany Department of the California Academy of Sciences, San Francisco, and after that, until her retirement in 1960, she was on the staff of the Western Regional Research Laboratory, U.S.D.A., Albany, California.

Mrs. Bracelin (née Nina Floy Perry) was born 24 March 1890 at Star Lake, Minnesota. She died in Berkeley, California, on 8 July 1973. She is remembered as a cheerful, friendly person, ever helpful to others, with a great capacity for work that was well done. Four plants were named in her honor: *Cordia Braceliniae* I. M. Johnston, *Fuchsia Braceliniae* Munz, *Salix lasiolepis* var. *Braceliniae* Ball, *Vochysia Braceliniae* Standley.—Annetta M. Carter, Department of Botany, University of California, Berkeley 94720.

White Fir in the Mountains of Eastern Mojave Desert of California.—During recent floristic surveys of the Providence, New York, and Clark mountains in the eastern Mojave Desert, a small, previously unrecorded population of white fir [*Abies concolor* (Gord. et Glend.) Lindl.] was located near the summit of the New York Mountains. Although white fir is wide ranging in western North America, occurring from central Oregon and Colorado south to Mexico, in the Mojave Desert it is known only from the Charleston (Spring), Clark, Kingston, and now the New York Mountains. These populations are of interest because they are disjunct islands of coniferous forest lying between the Rocky Mountains and the mountains of

southern California. The white firs and their associates represent remnants of perhaps a more widespread coniferous forest. The extent of these former coniferous forests is unknown.

The population of white fir in the New York Mountains occurs in a small, protected, very steep, north-facing granitic ravine just below the crest of the range. It lies 0.6 km slightly east of true north from the summit and 0.6 km west of the mine in Keystone Canyon at 2073–2164 m (6800–7100 ft). The stand occurs over approximately 0.8 hectares (2 acres) and consists of only thirty trees, the largest of which measured 71 cm (28 in) DBH and approximately 17 m (55 ft) in height. All size classes were represented in the population; nearly half were less than 10 cm DBH, nine were over 40 cm DBH.

In the Kingston Mountains, white fir stands occur in two narrow, very steep, north-facing, granitic canyons north of Kingston Peak. The white firs are scattered over about 12 hectares (30 acres) from 1950–2195 m (6400–7200 ft). The populations were estimated to contain about 150 individuals. The largest tree observed measured 86 cm (34 in) DBH; the tallest tree was about 20 m (66 ft) high. Again all size classes were present but, as in the New York Mountain population, seedlings were rare.

White fir is much more extensive in the Clark Mountains, occurring in two separate canyons and upper intervening areas on the steep, north-facing limestone slopes and on the limestone wall below the crest of Clark Mountain. The stand covers about 65 hectares (160 acres), much larger than designated by Miller (Condor 42:161–163), and contains over 1000 individuals between 1905 and 2347 m (6250–7700 ft). Of the trees sampled the largest was 87 cm (35 in) DBH and the tallest was 17 m (56 ft). Approximately 30 percent were less than 10 cm DBH. The population is represented by all size classes, although more frequently by the smaller classes. No seedlings with juvenile foliage were observed.

White fir is much more common in the Charleston Mountains where Clokey (Univ. Calif. Pub. Bot. 24, 1951) notes its occurrence from 2270–3300 m (7450–10800 ft).

The white fir in the eastern Mojave Desert represents the Rocky Mountain form, which has been designated as *A. concolor* var. *lowiana* (Gord.) Lemmon. This taxon, which is usually not recognized by North American botanists, differs in both morphological and chemical characteristics from the Sierran form (var. *concolor*). The Rocky Mountain form is morphologically characterized by having leaves reoriented by general curvature of the entire leaf rather than a more localized twist at the base as in the Sierran form (Critchfield, pers. comm.). Zavarin and Snajberk (Phytochemistry 4:141–148) cite distinct quantitative differences in terpenes between these forms. Critchfield notes that influence of the Rocky Mountain form occurs as far east into California as the Tehachapi Mountains.

The white fir populations in the three California ranges are limited to the more mesic, north-facing slopes and represent persisting, relict stands of mesophytic species. Though Wells and Burger (Science 155:1640–1647) have provided evidence from a study of wood rat middens that there may have been a past continuance of juniper woodland between some of the ranges in the Mojave Desert, they note that there is no evidence of a continuous distribution of the more mesophytic vegetations between these ranges and the rocky or southern Californian mountains for the past 40,000 years. They further note the uneven pattern of distribution of a few dominant species associated with the white fir in the Mojave Desert ranges and the absence of white fir from the Panamint Mountains even though this range contains other mesophytic species commonly associated with white fir, e.g., *Acer glabrum* var. *diffusum* and *Betula fontinalis*, as well as rather limited areas of the next higher vegetation zone of bristle-cone and limber pines. The uneven distribution of plant species between these ranges is shown even more by other perennial associates. Plants associated with the white fir populations on the three California ranges, New York, Clark, and Kingston, are indicated in tabular form in Table 1. Occurrence of these

TABLE 1. DISTRIBUTION OF PLANTS ASSOCIATED WITH WHITE FIR ON THE NEW YORK (NY), CLARK (CL), AND KINGSTON (KN) MOUNTAINS OF CALIFORNIA AND THE CHARLESTON (SPRING) MOUNTAINS (CH) of NEVADA. Additional range of each taxon in the Colorado Plateau (CO), Transverse Ranges (TR), Peninsular Ranges (PR), Cascades (CC), Sierra Nevada (SN), Great Basin (GB), Columbia Plateau (CB), Rocky Mountains (RM), and Sonoran-Chihuahuan Desert (SC) and further to the east (E) is included. Data obtained from various floras. The taxa are arranged alphabetically within groups. Species occurring in the ranges but not associated with white fir are indicated by an asterisk. Certain species of widespread occurrence throughout the ranges are not indicated, e.g., *Ephreda viridis. Sedum niveum* on the New York Mountains represents a range extension from the San Bernardino-Santa Rosa Mountains. Nomenclature follows Munz, *A flora of Southern California,* 1974.

	NY	CL	KN	CH	—	CO	TR	PR	CC	SN	GB	CD	CB	RM	SC	E
Endemic species																
Erigonum heermannii var. *floccosum*	NY	CL		CH												
Potentilla patellifera			KN													
Species ranging westward																
Amelanchier covillei		CL		CH							GB					
Eriogonum heermannii var. *sulcatum*	NY	CL		CH							GB					
Eriogonum panamintense var. *panamintense*		CL	KN	CH							GB					
Galium matthewsii			KN								GB					
Galium parishii	NY	CL	KN				TR	PR			GB					
Halimolobos diffusa var. *jaegeri*	NY	CL	KN							SN	GB					
Heuchera rubescens var. *pachypoda*	NY	CL	KN	CH						SN	GB					
Hymenopappus filifolius var. *eriopodus*	NY	CL									GB					
Leptodactylon pungens ssp. *hallii*		CL	KN	CH			TR	PR			GB					
Monardella linoides ssp. *linoides*	NY	CL	KN				TR	PR		SN	GB					
Sedum niveum	NY						TR	PR								

	NY	CL	KN	CH	—	CO	TR	PR	CC	SN	GB	CD	CB	RM	SC	E
Species ranging eastward																
Eriogonum umbellatum var. *ferrissii*	NY	CL	KN	CH							GB	CD				
Galium munzii		CL									GB	CD				
Galium wrightii		CL									GB	CD			SC	
Fraxinus anomala	NY	CL		CH							GB	CD			SC	E
Ipomopsis aggregata ssp. *arizonica*	NY	CL	KN	CH							GB	CD				
Juniperus osteosperma	NY	CL	KN	CH							GB	CD	CB	RM		
Lomatium parryi	NY	CL	KN	CH							GB	CD				
Penstemon eatonii	NY	CL	KN	CH							GB	CD				
Petradoria pumila	NY	CL	KN	CH							GB	CD	CB	RM	SC	
Petrophytum caespitosum	NY	CL		CH							GB	CD	CB	RM	SC	E
Pinus edulis	NY										GB	CD		RM	SC	
Silene verecunda ssp. *andersonii*	NY		KN	CH							GB	CD				
Zauschneria garrettii	NY		KN								GB	CD		RM		
Species of general distribution																
Chrysothamnus viscidiflorus ssp. *viscidiflorus*			KN	CH			TR	PR	CC	SN	GB		CB	RM		
Acer glabrum var. *diffusum*		CL	KN	CH			TR	PR		SN	GB	CD				
Amelanchier utahensis			KN	CH			TR	PR			GB	CD	CB	RM		
Haplopappus cuneatus	NY	*	KN	CH			TR	PR		SN	GB	CD				
Holodiscus microphyllus var. *microphyllus*	NY	CL	KN	CH			TR			SN	GB	CD		RM		
Opuntia erinacea var. *erinacea*	NY	CL	KN	CH				PR			GB	CD				
Philadelphus microphyllus ssp. *stramineus*	NY	CL	KN	CH				PR			GB	CD				
Pinus monophylla	*	CL	KN	CH				PR		SN	GB	CD				
Quercus chrysolepis	NY					CO	TR	PR		SN	GB	CD			SC	
Quercus turbinella var. *turbinella*	NY							PR			GB	CD			SC	
Ribes cereum		CL	KN	CH				PR	CC	SN	GB	CD	CB	RM		
Ribes velutinum var. *glanduliferum*	NY		KN				TR				GB	CD				
Sambucus mexicana		CL		CH			TR			SN	GB	CD			SC	

taxa in the Charleston Mountains is also included for comparison (Clokey ibid.), as is the general range of each species outside the area. It must also be noted that the populations of white fir on the New York and Kingston Mountains occur on granite substrate, while those in the Clark Mountains occur on limestone.

Of the thirty-nine species observed in association with the white firs on the New York, Kingston, and Clark mountains, two are endemic to these ranges and the remaining are rather equally divided between those that range to (1) west, e.g., Sierra Nevada and Transverse ranges, (2) east (Colorado Plateau and beyond), and (3) both east and west of this portion of the Mojave Desert. The percentage of species shared by any two mountains ranges from 44 to 61 percent and is higher between the Charleston Mountains and Clark and Kingston Mountains and lower between the New York Mountains and the Kingston and Charleston Mountains. Only nine (23%) of the species occur on all four ranges. Of interest is the uneven distribution of some of the more conspicuous species; for example, *Quercus chrysolepis, Q. turbinella,* and *Pinus edulis* are known only from the New York Mountains. The moderate floristic discontinuity between the more mesic habitats on these ranges would seem to support considerations that the white fir and associated species have probably never been continuous between the ranges in the past.—James Henrickson and Barry Prigge, Department of Biology, California State University, Los Angeles 90032.

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RE-EVALUATION OF BRACT MORPHOLOGY IN TAXONOMY OF CORDYLANTHUS (SCROPHULARIACEAE)

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Cordylanthus taxonomy has traditionally relied heavily on the shape of the outer bract. One to several outer bracts are present at the base of each inflorescence, which in the species considered in the present study is reduced to a single flower (fig. 1 B and C) with one or two outer bracts. Of no concern here is the floral bract (fig. 1 B and D), which subtends each flower, resembles the ligulate calyx (fig. 1 E), and is remarkably uniform throughout most of *Cordylanthus*. The two existing treatments of the genus (Ferris, 1918; Pennell, 1951) use presence or absence of lobing of outer bracts as a character for separating species. During our comparative studies in the genus, we came to question whether this feature should receive such taxonomic weight. Entities that we judged to be closely related on the basis of a group of shared characters became widely separated taxonomically when outer bract shape, especially presence or absence of lateral lobing, was accorded overriding importance. We suspected that these bract variants might be interfertile and that the presence or absence of lobing of outer bracts is controlled by only small genic differences.

To test this hypothesis, two "species", showing general morphological similarity except for outer bract form, were artificially hybridized. *Cordylanthus brunneus* (Jeps.) Pennell, a fairly localized endemic of serpentine regions of Lake, Napa, and Sonoma Counties, California, has entire outer bracts (fig. 1 C). *Cordylanthus capillaris* Pennell (1950), known only from two populations in the Monte Rio-Occidental region in Sonoma County, about 40 km from the nearest population of *C. brunneus* and also on serpentine soil (see Bacigalupi, 1966), has bracts with one pair of lateral lobes (fig. 1 C).

These two species show other minor differences. Leaves as well as outer bracts of *C. brunneus* are narrowly linear while those of *C. capillaris* are filiform. The corolla of *C. brunneus* is mottled and striated with purplish maroon while in *C. capillaris* this coloration forms a solid band (fig. 1 F and G). In *C. brunneus* outer bracts and upper stems are sparsely glandular-puberulent while in *C. capillaris* they are glabrous. Lateral lobing of primary stem leaves, while not uncommon in *C. brunneus,* is a consistent feature in *C. capillaris* (fig. 1 A).

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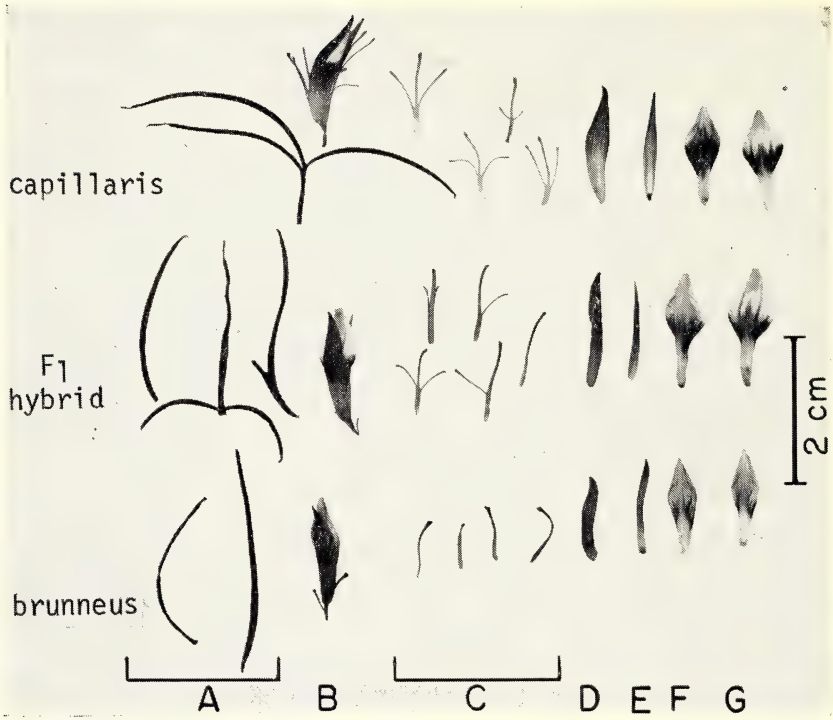

FIG. 1. Photographs of leaves, bracts, and flowers of *Cordylanthus brunneus, C. capillaris,* and their F_1 hybrid. Column A, leaf; B, single-flowered inflorescence with single floral bract, 1–2 outer bracts and 1 subtending bract; C, outer bracts; D, floral bract; E, calyx; F, dorsal view of corolla; G, ventral view of corolla.

METHODS

Parental strains were raised from seed obtained from type localities of each species. *Helianthus annuus* was used as host for these annual root hemi-parasites (Chuang and Heckard, 1971). Seed set is extremely rare on cultured plants lacking natural pollinators, although the plants are capable of some self-fertilization when artificially selfed. Higher seed set was obtained by crossing between different individuals. For this reason the F_2 generation was obtained by intercrossing F_1 plants rather than by selfing. One F_1 plant (number 3) was used as the female parent but pollen was taken indiscriminately from the other four F_1 plants. Likewise, the F_1 hybrids were obtained by using pollen from several plants of *C. capillaris* on the stigmas of one plant of *C. brunneus*. About 8–15 seeds per capsule are produced in nature but our artificial techniques yielded usually fewer than six seeds per capsule. Because of difficulty in making artificial hybridizations, the number of seeds produced per capsule is not believed to be a reliable criterion of interfertility. Estimates of fertility were made on pollen by examining ca 500 grains from at least three flowers per plant stained in lactophenol and cotton-blue.

Cytological preparations were made from aceto-carmine smears of microsporocytes preserved in a solution of chloroform: ethanol: glacial acetic acid (4:3:1, v/v).

Voucher specimens (JEPS and ISU) are as follows: *Cordylanthus brunneus* parent, Napa-Sonoma County line, N side of Mt. St. Helena, *Chuang 6843*; *C. capillaris* parent, Sonoma Co., 2.7 mi NE of Occidental, *Chuang 6845;* F_1 hybrids, *Heckard 71–7*; F_2 hybrids, *Heckard 72–31.*

Results

Five plants of the F_1 generation were raised to maturity. Each had bract types of both parental plants in addition to an intermediate type with only one lateral lobe (fig. 1 C). Table 1 lists the number of these bract types for each of the five F_1 plants based on one count made towards the end of the flowering period. Usually there was only one outer bract per inflorescence (excluding the subtending bract of the inflorescence, which is similar to the upper leaves in lobing pattern). When occasionally two outer bracts were present, they were either the same or one was intermediate. Also listed for each F_1 plant is an estimate of pollen fertility as determined by pollen stainability. The average pollen fertility for the five F_1 plants was 75 percent, which can be compared with an average of 93 percent for the parents growing under similar conditions.

The 19 plants of the F_2 generation had a higher pollen fertility average, 91 percent, individual plants ranging from 85 to 98 percent. Some of the F_2 plants (Table 2) were like the parental types, with either entire or 2-lobed bracts, while others had combinations of two or three types. Rather than list the numbers of bract types in each of the F_2 plants, we have summarized the data to give the number of plants having each of the various bract conditions. It is perhaps noteworthy that of the six plants of the F_2 generation with all three bract types, five showed more inflorescences with the 2-lobed bract condition, whereas in the F_1 generation entire bracts outnumbered 2-lobed bracts.

Other characters mentioned earlier that show minor morphological differences between *C. brunneus* and *C. capillaris* were intermediate in

Table 1. Distribution of Outer Bract Types and Pollen Fertility in Five Plants of F_1 Generation of Cordylanthus brunneus–C. capillaris cross.

F_1 plant number	Bract condition			Pollen stainability
	entire	1 lateral lobe	2 lateral lobes	
1	113	18	21	78%
2	103	13	4	70%
3	151	114	89	80%
4	22	17	21	62%
5	180	82	70	82%

TABLE 2. SUMMARY OF OUTER BRACT LOBING IN 19 PLANTS OF F_2 GENERATION OF CORDYLANTHUS BRUNNEUS–C. CAPILLARIS CROSS.

Number of lateral lobes in bracts	Number of plants	Phenotypic summary
0 (as *C. brunneus*)	8	8 plants with entire bracts
0, 1, and 2	6	10 plants with intermediate conditions
0 and 1	2	
1 and 2	2	
2 (as *C. capillaris*)	1	1 plant with two lateral lobes

the F_1 plants, while intermediate and parental conditions appeared in the F_2 generation. No attempt was made to analyze inheritance of these features.

Chromosome numbers of $n = 14$ are reported here for the first time in both parents. No meiotic irregularity was seen in prophase and metaphase of the F_1 hybrids; normal segregation of 14 chromosomes occurred in anaphase.

DISCUSSION AND CONCLUSIONS

The high degree of interfertility between the bract-variants "*brunneus*" and "*capillaris*" and evidence that only minor genic differences control bract lobing indicate that these forms should be included in the same species. We will propose in our forthcoming taxonomic revision of subg. *Cordylanthus* that each variant be given subspecific status. Similarly, *C. viscidus* (Howell) Pennell of northern California and southern Oregon should be treated as conspecific with *C. tenuis* Gray of the Sierra Nevada, from which it differs largely in having lobed outer bracts. Likewise, *C. pilosus* Gray of the California Coast Ranges, with entire bracts, and *C. hansenii* (Ferris) Macbride of the Sierra Nevada foothills, with lobed bracts, are probably conspecific, as is suggested by the presence of intergrades (California, Shasta County, *Heckard 2799,* JEPS) in the region where their ranges juxtapose. These intergrades include individual plants with both bract types.

The small number of plants in the F_2 generation of the *C. brunneus -capillaris* cross did not allow analysis of the precise inheritance mechanism for bract shape. The segregation ratios of the F_2 plants [eight with entire bracts: ten intermediates: one 2-lobed (Table 2)] indicate that multiple genes may be operating with dominance for entire bracts. This is particularly suggested by the presence of only one plant with all 2-lobed bracts (as *capillaris*) and eight plants with entire bracts (as *brunneus*).

The F_1 plants that produced both parental bract types as well as intermediate forms are postulated to have genes that in the heterozygous condition were able to effect only partial expression of the dominant unlobed bract condition. The factors responsible for determining which particular lobing pattern develops in the embryonic stage are unknown.

The question of the origin of lobed bracts in the isolated southern populations *(C. capillaris)* merits consideration. The mutation producing lobing in outer bracts would seemingly not require a major change since the mechanism for producing a similar lobing in the leaves is already present in some plants of *C. brunneus*. Incorporation of this mutation into the population can be postulated to have come about by natural selection. However, the selective advantage of the lobed over the entire bract is not evident and a plausible alternative would be genetic drift or random fixation (Wright, 1931; Dobzhansky, 1941) of non-adaptive features. The necessary prerequisites for random fixation in plants, as discussed by Stebbins (1950), could have been present in this case: a small, isolated population confined to open barrens of a small serpentine "island". If genes for lobed bracts arose by mutation in such a population, this feature could become established by chance survival of mutant types during a period of severe stress when the population was highly reduced and only seed of the mutant survived. Reduction in population size to zero or nearly so does occur in the genus, as was observed in *C. helleri* (Ferris) Macbride of the western Great Basin when seed germination was reduced apparently by drought (Chuang and Heckard, 1971).

Acknowledgments

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REMNANT SEASHORE VEGETATION OF NORTHWEST COSTA RICA

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The massive literature on coastal vegetation of the world leaves the Pacific side of Central America almost untouched. Presence of mangroves and a few other strand species has been reported from the Golfo de Panamá (Johnston, 1949) and the Golfo Dulce (Allen, 1956). A single schematic profile of mangrove zonation is available from the coast of El Salvador (Gierloff-Emden, 1974); the rest of the coastal vegetation is blank for 2,000 km between the rainforest region of Golfo Dulce and the thorn-scrub region of western Mexico, where reconnaissance studies again list some coastal species (Turner, 1960; Rzedowski and McVaugh, 1966). The transects to be discussed here sample a small, 30 km long sector of that blank, located on the seasonally dry Guanacaste coast. These transects, done in 1972, were intended to salvage information on what remained of the spontaneous seashore vegetation before it was too late.

With Costa Rican government encouragement, this beautiful and formerly inaccessible coast is being promoted as a prime attraction for local and foreign tourists and retired people. In 1972, the largest beach in the sector was being internationally advertised as "Playa Grande Estates, the American way of life brought to Costa Rica by American developers". The coastal thicket had been bulldozed to stake out sites for 400 homes, a luxury hotel, and a country club. For a long time the region has had a few modest beach resorts, such as Playas del Coco, with dry weather road access but they were far apart and wild stretches lay between. New airstrips and all-weather roads are rapidly opening the wild stretches to development. Presumably the native seashore vegetation will soon give way to the pool of cosmopolitan ornamentals and weedy plants that have been spread around the tropics since Columbus. At Playas del Coco, for example, the beach houses are surrounded by East Indian almonds (*Terminalia catappa*), Madagascar flamboyants (*Delonix regia*), South Pacific crotons (*Codiaeum variegatum*), African Bermuda grass and tamarinds (*Cynodon dactylon* and *Tamarindus indica*), and Indo-Pacific coconuts (*Cocos nucifera*).

Whether coconut palms are members of the natural vegetation of this coast is unclear. When Balboa crossed the isthmus, there were wild coconut groves farther south on the Pacific coast of Costa Rica and Panamá, evidently volunteers from sea-drifted nuts (Patiño, 1963; Sauer, 1971). The prevailing current would have carried nuts from those groves up along the Guanacaste coast, so that the species may have grown here spontaneously also. If so, it is one member of the natural vegetation that is becoming commoner along the sea as a result of human planting.

Vegetational transects were run at right angles to the shore in the form of continuous belts, 1 m wide, in eight sectors between Boca Venado (10°9′ N) and Bahia de Culebra (10°36′ N). Multiple transects, spaced at least 100 m apart, were made in physiographically complex sectors. Type of substrate, species present, estimated cover, and maximum plant height were recorded for each square meter along the transects. Each transect was unique in detail but a few selected transects (figs. 1–5) show most of the range of diversity encountered. Transects were placed without regard to vegetational composition except that areas of obvious severe artificial disturbance were avoided.

It should not be implied that much of the coastal vegetation was in a pristine state at the time of study. The Guanacaste region was the home of ancient high civilizations that gave way during the Spanish colonial period to small cattle ranches and subsistence farms. The seasonal forest has been greatly affected by clearing for pasture and shifting cultivation. However, the ranchers left some fringes of vegetation along tidal estuaries, beaches, and rocky headlands; these will be discussed in that order.

Intertidal Woodland

In spite of a mean tidal range of about 2 m, the rugged topography and steep stream gradients confine mangroves to small stands that do not compare in extent with the swamps on the inland side of the Nicoya peninsula. However, the dominant species are the same: *Rhizophora mangle, Avicennia germinans,* and *Laguncularia racemosa.* Less expectedly, *Laguncularia* trees were also found rooted in rock crevices that are washed by waves on the shore of the large, open Bahia de Tamarindo. Elsewhere, on fairly open sandy beaches, some other trees and shrubs were also found growing within reach of the waves at high tide: *Hippomane mancinella* on Playa Hermosa and Playa Panamá, *Hibiscus tiliaceus* at Boca Venado, and *Conocarpus erectus* on Punta San Francisco. In the Caribbean, these three species are commonly associated with mangroves on inner margins of tidal swamps; they also grow on less sheltered coast there, but only above the high tide mark.

Sand Flat Vegetation

Beach progradation by wave upwash has built stabilized sand flats or plateaux at the heads of many coves and bays along this coast. The sand ranges from tan to nearly black, depending on proportions of quartz, shell, and heavy minerals.

On the most sheltered bays, the sand flat vegetation, behind whatever intertidal trees may be present, shows no special coastal character in either physiognomy or floristics. The dominant species are all common members of inland thorn scrub and seasonal woodland communities. Most of them range widely through Central America, Mexico, northern South America, and the West Indies. The mesquite (*Prosopis juliflora*),

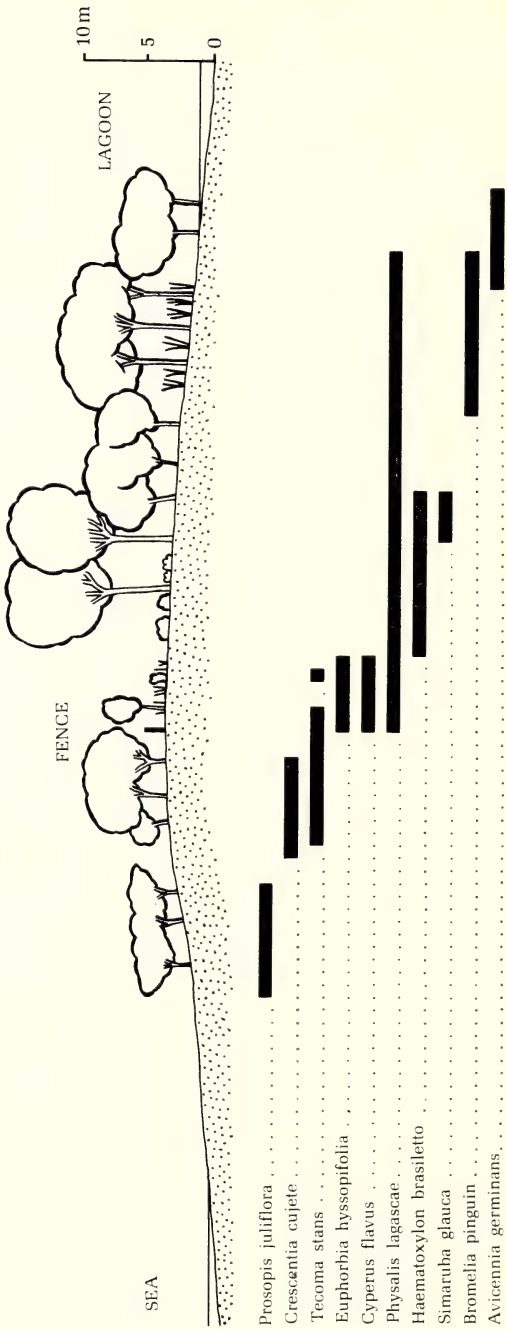

FIG. 1. Transect at Playa Hermosa (10°35′ N). Wave-built ridge of dark, heavy mineral sand at head of bay between high, rocky headlands, open to ocean toward NW over about 50° of arc. Estuary of small stream behind. Transect near center of 1 km long beach in area disturbed by clearing and pasturing, property of small ranch at end of old wagon road. Gentle waves at time of study. (Vertical and horizontal scales are equal on all profiles.)

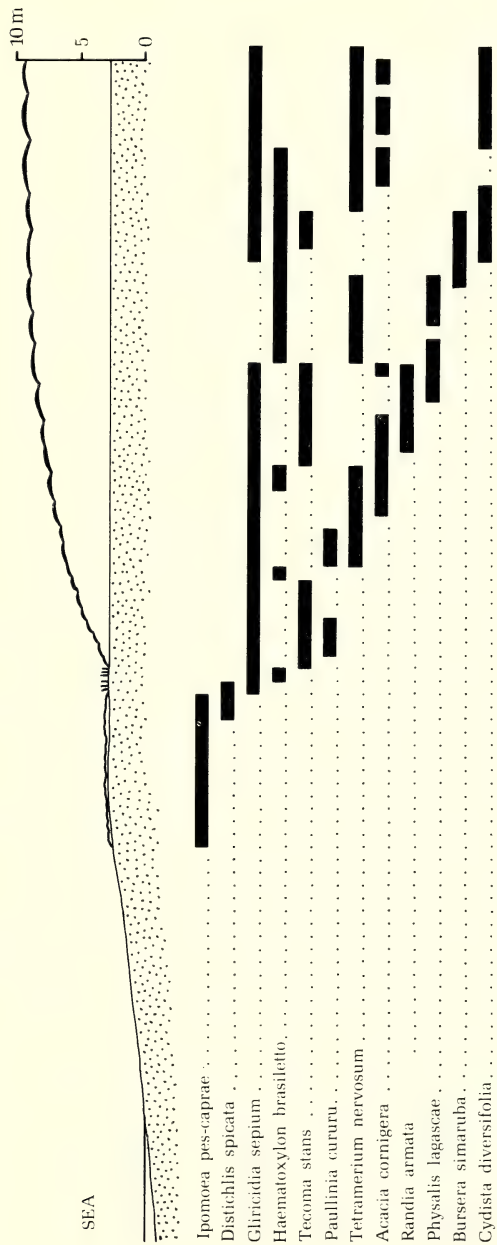

FIG. 2. Transect at Playa Grande (10°19′ N). Sand flat with much shell and some heavy minerals at head of wide bay, open to ocean over about 100° of arc. Transect beyond edge of bulldozed area near south end of 3 km long beach. Thicket has similar composition for nearly 500 m farther inland to edge of estuary fringed by *Capparis odoratissima* trees. On 1955 aerial photograph, this sand flat appears as cleared pasture. Moderate surf at time of study.

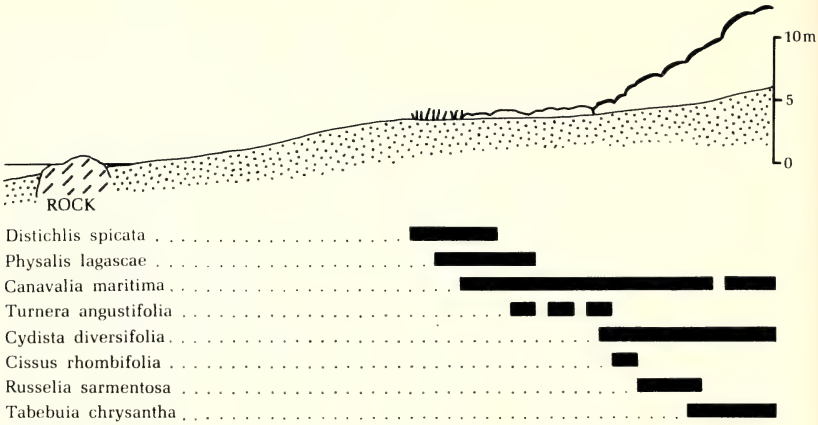

FIG. 3. Transect at Punta Cerritos (10°9′ N). Cove beach of dark, heavy mineral sand and shell on low, rocky point, open to ocean toward SW over about 120° of arc. Moderately heavy surf at time of study.

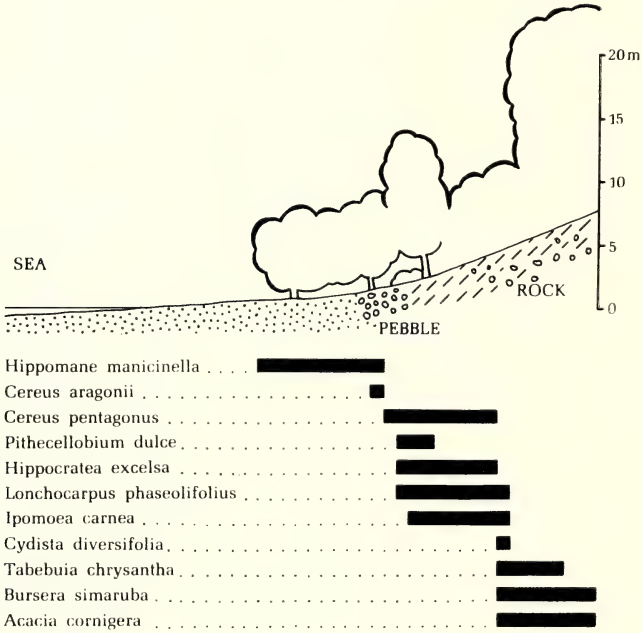

FIG. 4. Transect at Playa Pedregosa (10°34′ N). Narrow beach of heavy mineral sand and a little shell material over metamorphic bedrock, open to ocean toward NW over about 50° of arc. Transect half way between head of bay and tip of headland. Moderate waves at time of study.

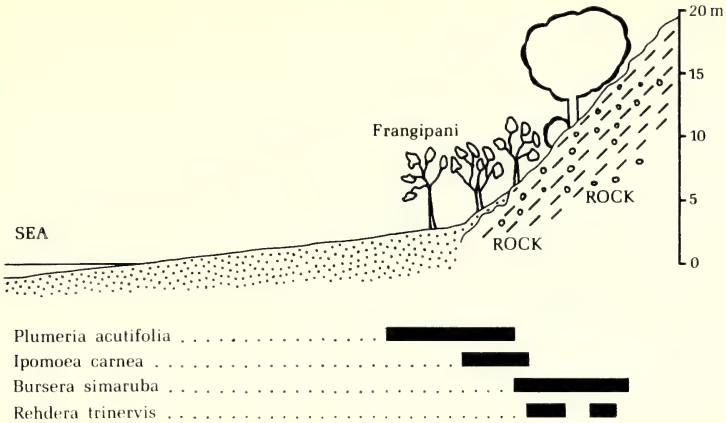

FIG. 5. Transect at Playas del Coco (10°33′ N). Coral rubble and shell mixed with dark sand over metamorphic bedrock, open to ocean toward N over about 15° of arc. Transect on S side of Bahia El Coco half way between its head and Punta Centinela. Gentle waves at time of study.

calabash tree (*Crescentia cujete*), and other species on a Playa Hermosa transect (fig. 1) are examples, as are *Pithecellobium dulce* and *Bursera simaruba,* which do not appear on this particular transect but were common dominants on several sheltered sand flats.

On more exposed shorelines, the sand flat vegetation displays rudiments of the classic beach zonation, with outpost vines and creepers backed by a spray-shorn thicket (figs. 2–3). The outpost zone is exceptionally narrow and poor in species. It has the pantropical beach morning-glory and sea-bean (*Ipomoea pes-caprae* and *Canavalia maritima*) and the common New World seashore saltgrass (*Distichlis spicata*). The few other species found in this zone are primarily pioneer herbs of open inland sites, the most abundant being *Physalis lagascae, Euphorbia dioica,* and *Pectis grandiflora.* In the thicket behind the outpost zone, the only abundant peculiarly coastal species is the pantropical gray nicker-bean (*Caesalpinia bonducella*). These thickets, like those on more sheltered bays, are dominated by species that range widely through tropical America in inland scrub formations, especially on limestone.

Rocky Promontories

Headlands between the bays have outcrops of metamorphic rock and talus slopes. These are the habitat of two primarily coastal cacti, the wide-ranging *Cereus pentagonus* and the endemic *C. aragonii.* On the most exposed headlands, these cacti are joined by two succulent monocots (*Fourcroya cabuya* and *Bromelia pinguin*) that are shared with rocky inland sites. On less exposed slopes, the cacti are joined by frangipani (*Plumeria acutifolia*) and other species shared with sand flats and inland scrub (figs. 4–5).

Discussion and Conclusions

This region's impoverished seashore flora can hardly be blamed on geographic isolation and lack of insemination. Several strictly coastal Atlantic-Caribbean species are represented, namely the three mangroves and two associates, *Hippomane mancinella* and *Conocarpus erectus*. These were evidently dispersed by ocean currents before interposition of the present isthmus; other members of the rich Caribbean seashore flora could presumably have immigrated the same way had the region been hospitable to them. We know in fact that lack of dispersal is not responsible for absence of the most important of all Caribbean seashore species, the sea-grape (*Coccoloba uvifera*). This species was deliberately introduced to the Pacific coast and old trees are commonly seen planted around beach houses but the seedlings do not establish themselves in natural habitats here.

Four other species adapted for long-range ocean dispersal are shared not only with the Caribbean but with tropical coasts in general: *Canavalia maritima, Caesalpinia bonducella, Hibiscus tiliaceus,* and *Ipomoea pes-caprae*. These four, like the coconut, may have arrived from the west across the Pacific. They are all present on Cocos Island off Panamá (Fosberg and Klawe, 1966), where the Equatorial Counter Current coming from the west turns northward to sweep along this coast.

I believe the rudimentary character of the distinctively coastal vegetation of this coast is due simply to lack of storms and of onshore winds. Tropical cyclones occasionally develop in this general region but they usually form well offshore and move far away to the west before generating gale or hurricane force winds (U.S. Navy Hydrographic Office, 1964). Heavy surf must be rare as the upper limit of old, stranded drift is barely above normal high tide mark. The mangroves and associates noted as standing within wave reach on only partly sheltered beaches also bear witness to absence of high energy waves. In other words, the storm beach zone, the normal habitat of much of the world's coastal pioneer flora, is virtually missing here.

Ths coast also provides peculiarly little opportunity for the salt spray community. During the dry season, when salt spray should be most effective in driving back ordinary inland pioneer species, winds are prevailingly from the northeast, i.e., offshore. During the rainy season, from May to October, wind directions are more variable but velocities are normally weak. Some spray shear is evident on thicket canopies on exposed headlands and behind the more open beaches but a very little spray might produce this effect on the thin-leaved species present. In short, a rugged, storm-free, lee coast offers a vanishingly narrow habitat for specialized seashore plants.

However, it does not follow that this coast has played an insignificant role in evolution and migration of pioneer plants. The edge of the land offers pioneer species an opening that is relatively permanent and spa-

tially continuous compared to many of the habitats they colonize in inland succession. Even if relatively small, coastal subpopulations may have been crucial links in spread and survival of their species.

ACKNOWLEDGMENTS

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REVISION OF PECTIS SECT. HETEROPECTIS (COMPOSITAE: TAGETEAE)

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Pectis L. sect. *Heteropectis* A. Gray is one of the smallest and most geographically restricted sections of *Pectis*. Comprising only two species, sect. *Heteropectis* is centered in the Sonoran Desert and only slightly exceeds the boundaries of that zone. No other section of the genus is known to occupy such a limited geographical range.

A unique feature of sect. *Heteropectis* is the structure of the pappus awns, which are unlike those of any other taxon in the genus, or indeed, in all of the Tageteae. The awns are retrorsely barbed in a manner similar to that of the pappus awns of *Bidens* (Heliantheae: Coreopsidinae). In *Bidens,* the barbed awns are an adaptation that promotes fruit dispersal by animals (Daubenmire, 1974). The pappus of the species of sect. *Heteropectis* may reflect a similar adaptation.

Taxonomic History

Gray (1849) originally described *Heteropectis* as a subgenus of *Pectis* and incorporated into this subgenus four species with aristate pappus: *P. coulteri* Harv. & Gray, *P. fastigiata* A. Gray, *P. filipes* Harv. & Gray, and *P. multiseta* Benth. In 1852, Gray amended his concept of *Heteropectis* by removing *P. fastigiata* and *P. filipes* and restricting it to taxa with retrorsely barbed pappus awns. At the same time, Gray also reduced *Heteropectis* to sectional rank with two species. In 1883, Gray further reduced *Heteropectis* by submerging it within sect. *Pectidium* (Less.) A. Gray. Fernald (1897) restored *Heteropectis* to subgeneric rank with three species: *P. coulteri, P. multiseta,* and the newly described *P. ambigua.* Rydberg (1916), although not recognizing infrageneric taxa other than species, grouped together four species referable to *Heteropectis: P. ambigua, P. bennettii* Klatt, *P. coulteri,* and *P. multiseta.*

The rank and circumscription of *Heteropectis* used in the present revision is based upon the emended concept of Gray (1852). Because the differences among various infrageneric species groups in *Pectis* seem insufficient for the establishment of subgenera, I am recognizing the sectional rather than subgeneric level for *Heteropectis* and similar taxa within the genus.

Chromosome Studies

Chromosome counts of $n = 12$ are reported here for the first time for all three taxa of sect. *Heteropectis* (Table 1). These new reports agree with the base chromosome number reported from species of other sections of the genus (Johnston and Turner, 1962; Keil, 1973). Apparently speciation in sect. *Heteropectis* has occurred entirely at the diploid level.

Sectional Relationships

Section *Heteropectis* is probably closely related to the larger and more widespread sect. *Pectothrix* A. Gray. Members of both sections are evolutionarily advanced taxa that are similar both morphologically (size, habit, head shape and size) and ecologically (emphemerals of desert regions). This similarity probably represents both parallel selective pressures and a common ancestry. Both sections were probably derived originally from ancestors that would be referable to a third section, *Lorentea* A. Gray. Some members of sect. *Lorentea* [e.g., *P. saturejaoides*

TABLE 1. NEW CHROMOSOME COUNTS FOR TAXA OF PECTIS SECT. HETEROPECTIS. Counts for *P. multiseta* var. *multiseta* and var. *ambigua* were made by Dr. A. M. Powell.

Pectis coulteri Harv. & Gray
Sonora, 14.8 mi E of Bahia de Guaymas, *Keil and Canne 8638B* (OS), $n = 12$; 7.2 mi SE of Navojoa, *Keil and Canne 8728* (OS), $n = 12$; 27 mi SE of Navojoa, *Keil and Canne 8734* (OS), $n = 12$.
Pectis multiseta Benth. var. *multiseta*
Baja California Sur, 7 mi W of La Palmilla, *Sikes and Babcock 243* (TEX), $n = 12$; 10 mi W of La Palmilla, *Sikes and Babcock 245* (TEX), $n = 12$.
Pectis multiseta Benth. var. *ambigua* (Fern.) Keil
Baja California Sur, 25 mi N of Todos Santos, *Sikes and Babcock 260* (TEX), $n = 12$; 26 mi N of Todos Santos, *Sikes and Babcock 261* (TEX), $n = 12$; 5 mi N of San Antonio, *Sikes and Babcock 267* (TEX), $n = 12$; 78 mi N of La Paz, *Sikes and Babcock 274* (TEX), $n = 12$.

(Mill.) Sch. Bip.] exhibit several features that are probably primitive in the genus (perennial habit, setose pappus, indefinite ray floret number, relatively mesic habitat). Section *Heteropectis* and sect. *Pectothrix* probably arose independently from different members of sect. *Lorentea*.

TAXONOMIC TREATMENT

PECTIS L. sect. HETEROPECTIS (A. Gray) A. Gray, Smithsonian Contr. Knowl. 3(5):83. 1852.—*Pectis* L. subg. *Heteropectis* A. Gray, Mem. Amer. Acad. Arts 4:62. 1849. Type species not designated. Lectotype (here chosen): *Pectis coulteri* Harv. & Gray.

Plants low, bushy, more-or-less pubescent, annual herbs, often strong-scented. Stems 1–35 cm long, much-branched. Leaves linear to oblong or narrowly obovate, bristly-ciliate on the margins, sometimes nearly to the apex, dotted on the undersurface with oil glands. Heads peduncled, solitary or in cymose clusters. Peduncles slender, bractless. Involucres cylindrical to campanulate. Phyllaries 5, linear to obovate, strongly keeled, dotted with oil glands. Ray florets 5; corollas yellow, with glabrous ligules and slender, glandular-puberulent tubes. Disc florets 7–20; corollas yellow, weakly bilabiate, glandular-puberulent below. Achenes of ray and disc similar, cylindric to clavate, black or dark brown, with a very small carpopodium, strigillose with short, uncinate trichomes. Pappus of 1–6 stout, retrorsely-barbed awns, or sometimes reduced to a low crown in the disc florets.

DISTRIBUTION: Central Sonora to Baja California Sur and northern Sinaloa from sea level to ca 500 m. One species, *P. coulteri*, occurs on the mainland areas of Sonora and Sinaloa; the other species, *P. multiseta*, is restricted to the southern portion of the Baja California peninsula (fig. 1). The disjunction between Baja California and the mainland is not unique to sect. *Heteropectis*. Six other species or species pairs within the genus have similar disjunctions, and a seventh has a continuous ditribution from the mainland to the peninsular region. For most of these

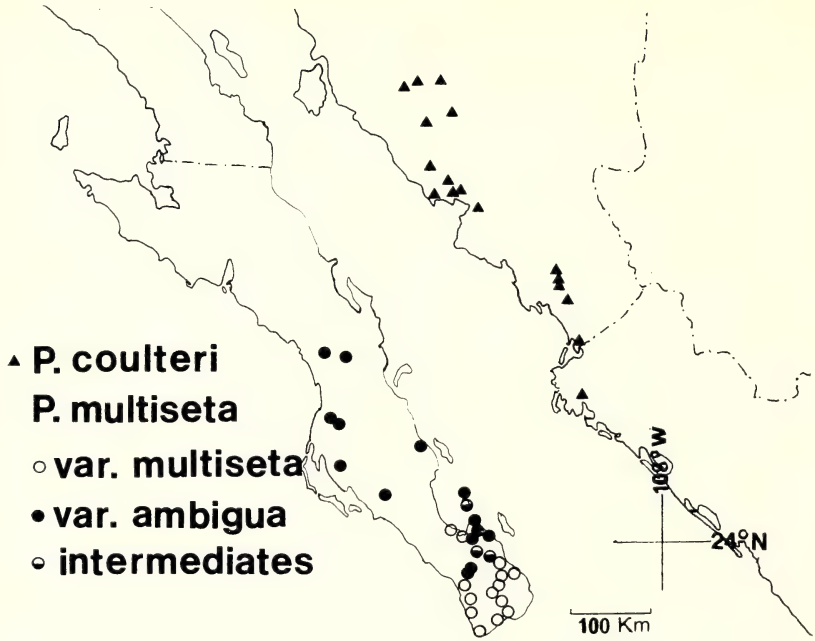

FIG. 1. Geographical distribution of *Pectis* sect. *Heteropectis*.

taxa, the mainland area appears to be the primary range of distribution. For sect. *Heteropectis,* with only two species, a certain determination of the primary range does not appear to be possible.

Key to *Pectis* sect. *Heteropectis*

1. Disc corollas bearing a sessile oil gland just below the apex of each tooth; some or all of the disc achenes often lacking an aristate pappus; plants of Baja California Sur. . . . . (2)
   2. Larger leaves usually 2–4 mm wide, bristly-serrate over most of their length; disc florets mostly 11–16; phyllaries imbricate. 1a. *P. multiseta* var. *multiseta*
   2. Larger leaves less than 2 mm wide, bearing bristles only below the middle; disc florets usually 7–12; phyllaries not imbricate. 1b. *P. multiseta* var. *ambigua*
1. Disc corollas eglandular; disc achenes all bearings a pappus of 2–6 awns; plants of Sonora and Sinaloa. . . . . 2. *P. coulteri*

1. PECTIS MULTISETA Benth., Bot. Voy. Sulphur 20. 1844. TYPE: Mexico, Baja California Sur, Cape San Lucas, without date, *R. B. Hinds s. n.* Holotype: K, not seen; Isotype: US!

Much-branched, often medicinally-scented, tap-rooted annual herbs

(sometimes persisting for more than one growing season). Stems 1–30 cm long, prostrate to ascending, solitary or more commonly several from the base, few- to many-branched above, often pseudodichotomous, stramineous to reddish or purplish, densely puberulent. Leaves linear to oblanceolate, 2–35 mm long, 0.5–4.0 mm wide, mucronate or bristle-tipped, punctate on the undersurface with scattered oil glands ca 0.1 mm diameter. Heads solitary or in leafy cymose clusters. Peduncles slender, puberulent. Involucres cylindric to campanulate. Phyllaries linear-oblanceolate to obovate, 3.5–7.0 mm long, 1–2 mm wide, strongly convex, round-keeled, punctate near the margins and along the midrib with linear-elliptic to oval oil glands, ciliolate on the margins toward the apex. Ray florets 5; corollas yellow or often tinged with red, 4.0–8.5 mm long, often punctate with one to several small oil glands, glandular-puberulent on the tube. Disc florets 1–20; corollas yellow, 2.5–4.0 mm long, equally or subequally 5-toothed, with each tooth punctate just below the apex with an oval oil gland, with the tube glandular puberulent. Achenes 2.5–4.5 mm long. Ray and disc pappus similar, of 1–4 retrorsely-barbed awns 1–2 mm long, or the pappus of some or all of the disc achenes reduced to a low crown.

Pectis multiseta occurs in the southern portions of Baja California Sur where it grows in a variety of dry, open habitats from sea level to ca 500 m (fig. 1). As presently treated, this species is restricted to the southern tip of the peninsula; var. *ambigua* is more northern in distribution and extends into some of the drier areas of the Sonoran Desert.

1a. PECTIS MULTISETA Benth. var. MULTISETA.

Pectis bennettii Klatt, Leopoldina 25:108. 1899. TYPE: Mexico, Baja California Sur, Prom. St. Lucas, without date, *Bennett 21*. Holotype: B (destroyed), photograph of holotype, F! US!; Isotype: GH!; Lectotype (here chosen): GH.

Stems 3–30 cm long. Leaves 5–35 mm long, 1–4 mm wide, serrate to above the middle and often to the apex with bristle-tipped teeth, glabrous or sparsely puberulent on the margins and midrib beneath. Heads solitary or in open cymose clusters. Peduncles 1–4 cm long. Involucres campanulate. Phyllaries imbricate, obovate, 3.5-5.5 mm long, 1–2 mm wide, broadly rounded, very obtuse, narrowly hyaline-margined, glabrous or puberulent. Ray corollas 6.0–8.5 mm long, with ovate lingules 5–7 mm long and 2–4 mm wide. Disc florets 11–20; corollas 3–4 mm long, equally 5-toothed or slightly bilabiate. Achenes 2.5–4.5 mm long. Pappus awns 1–2 mm long. Chromosome number: $n = 12$. Flowering from September to May following seasonal rainfall. Fig. 2.

REPRESENTATIVE SPECIMENS: Baja California Sur: 19.2 mi SW of San Jose del Cabo, 17 Dec 1947, *Carter, Alexander, and Kellogg 2241* (F, GH, MO, US); San Jose del Cabo, 23 Jan 1928, *Jones 24054* (ARIZ, F, GH, MO, NY, SD, TEX, UC); Buenavista, 6 Jan 1959, *Moran 6904* (ARIZ, CAS, GH, SD, TEX); 6.4 mi N of Todos Santos, 26 Dec 1958, *Porter 77* (ARIZ, CAS, GH, TEX, UC, US); Arroyo

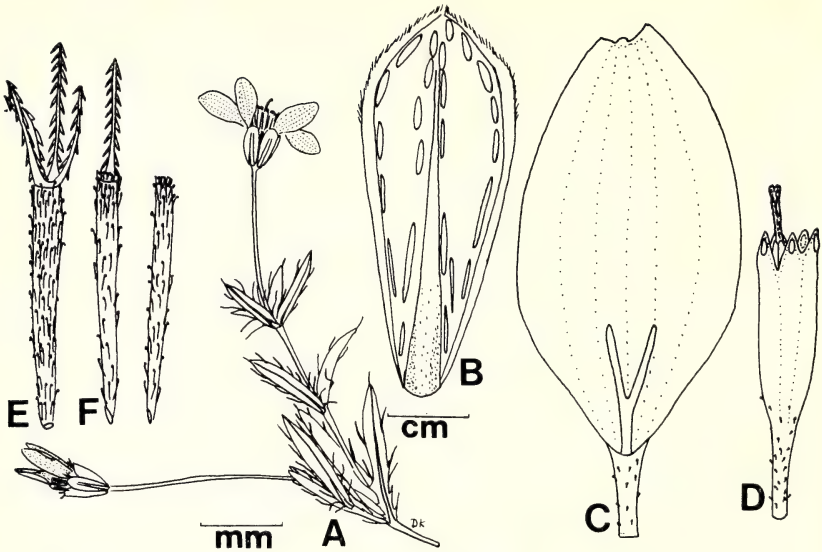

FIG. 2. *Pectis multiseta* var. *multiseta*. A, habit (*Dawson 1155*, F); B, phyllary; C, ray corolla; D, disc corolla; E, ray achene; F, disc achenes. B–F, same scale (*Porter 77*, TEX).

Salado, Jan–Mar 1901, *Purpus 387* (ARIZ, MO, UC, US); between Miraflores and San Jose del Cabo, 6–7 May 1931, *Wiggins 5672* (CAS, GH, LL, NY, UC, US); 39.5 mi S of La Paz, 24 Dec 1958, *Wiggins 14513* (ARIZ, CAS, UC); Cape San Lucas, Aug 1859–Jan 1860, *Xantus 44* (GH, NY, US).

Variety *multiseta* is quite common in the Cape Region of Baja California Sur and frequently grows nearly to the water's edge along the seashore; inland, the plants of this variety are scattered in open areas of the thorn forest and in disturbed sites.

1b. **Pectis multiseta** Benth. var. **ambigua** (Fern.) Keil, comb. et stat. nov.—*Pectis ambigua* Fern., Proc. Amer. Acad. Arts 33:84. 1897. Syntypes: Mexico, Baja California Sur, San Gregorio, Sep 1889, *T. S. Brandegee s.n.* (Syntype: GH!; Isosyntypes: UC! US); La Paz, 20 Jan–5 Feb 1890, *E. Palmer 23* (Syntype: GH!; Isosyntypes: NY (2)! US!); Lectotype (here chosen): *E. Palmer 23* (GH!).

Stems 1–20 cm long. Leaves 2–20 mm long, 0.5–2.0 mm wide, one to several setose-toothed, usually only below the middle, glabrous or puberulent on one or both surfaces. Heads solitary or in more-or-less congested cymose clusters. Peduncles 2–20 mm long. Involucres cylindric or narrowly campanulate. Phyllaries not or scarcely imbricate, linear-oblong, 3.5–7.0 mm long, 1.0–1.5 mm wide, very convex, very narrowly hyaline-margined, glabrous to densely puberulent. Ray corollas 4.0–6.5 mm long, with ovate ligules 1.0–2.5 mm wide. Disc florets 7–12; corollas

2.5–4.0 mm long, weakly bilabiate, with the narrow lobe ca twice the length of the teeth on the broad lobe. Achenes 3–4 mm long. Pappus awns 1 mm long. Chromosome number: $n = 12$. Flowering October to May following seasonal rains. Fig. 3.

Representative specimens: Baja California Sur: SE of La Paz on rd to Puente Coyote, 31 Mar 1949, *Carter 2603* (GH, US); Arroyo de Bachomo, 21 Mar 1973, *Carter et al. 5794* (UC); La Paz, 30 Mar 1931, *Collins, Kearney, and Kempton 57* (F, LL); 5.6 mi N of La Paz, 7 Oct 1964, *Hastings and Turner 64–139* (SD); 22 mi SW of Comundu, 18 Mar 1935, *Shreve 7134* (ARIZ, F, MO, UC, US); 13 mi N of El Refugio, 19 Mar 1935, *Shreve 7173* (ARIZ, F, UC, US); NW of El Triunfo, 29 Apr 1959, *Thomas 7690* (US); near Queretaro, 28 Apr 1931, *Wiggins 5514* (GH, LL, UC, US).

Two lines of evidence support the reduction of *Pectis ambigua* to varietal status within *P. multiseta*. In the area of sympatry between the two taxa, populations containing intermediate individuals are indicative of hybridization (e.g., *Wiggins 15339,* TEX). Additionally, populations of var. *ambigua* exhibit a clinal variation in leaf size and shape. The leaves in the southernmost populations are larger and bear more mar-

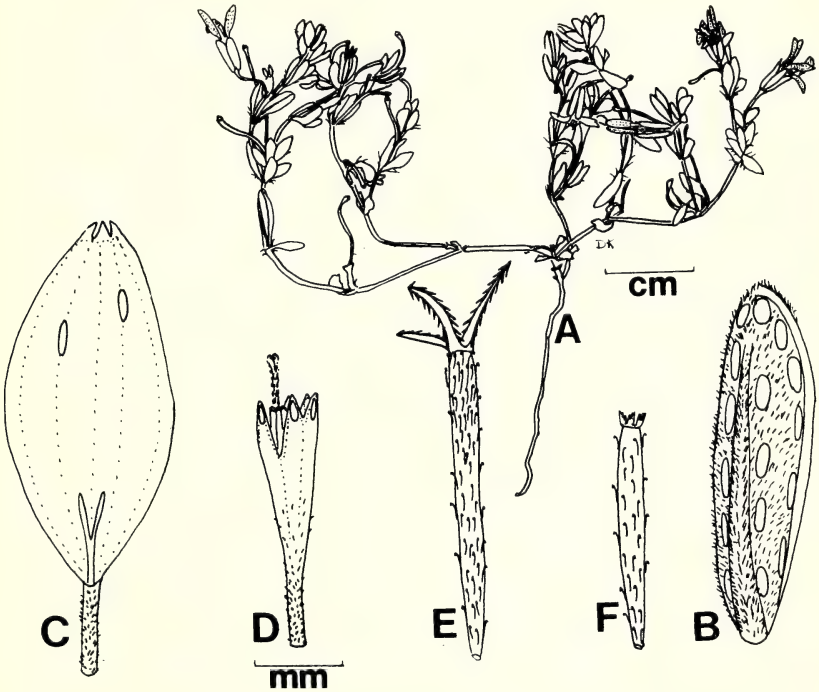

Fig. 3. *Pectis multiseta* var. *ambigua*. A, habit (*Wiggins 5514,* US); B, phyllary; C, ray corolla; D, disc corolla; E, ray achene; F, disc achene. B–F, same scale (*Sikes and Babcock 261,* TEX).

ginal bristles than those in the northern populations. This variation apparently represents introgression between the southern populations of var. *ambigua* and the larger-leaved var. *multiseta*.

2. Pectis coulteri Harv. & Gray in A. Gray, Mem. Amer. Acad. Arts 4:62. 1849. Type: "California" (probably actually collected in Sonora near Hermosillo or Guaymas), without date, *T. Coulter 331*. Holotype: TCD, not seen; Isotype (fragmentary): GH!

Plants bushy, medicinally-scented, tap-rooted, annual herbs (sometimes persisting through more than one growing season). Stems 5–35 cm long, solitary or more commonly several to many from near the base, pseudodichotomously branching above, stramineous or reddish-tinged, densely puberulent. Leaves linear, 5–30 mm long, 0.5–1.5 mm wide, mucronate, tapering slightly toward the base, with one or two pairs of setose-tipped basal teeth, otherwise entire, punctate on the margins with rounded oil glands up to 0.2 mm diameter and occasionally with a few scattered glands on the undersurface, glabrous to densely puberulent. Heads in open to condensed cymose clusters, Peduncles 5–20 mm long, densely puberulent. Involucres cylindric to very narrowly campanulate. Phyllaries 5, oblong to narrowly obovate, 4–7 mm long, 1.0–1.7 mm wide, strongly convex, keeled nearly to the tip, truncate at the base, gibbous, weakly longitudinally striate, very narrowly hyaline- or purplish-margined, dotted along the margin and along the upper half of the midrib with rounded oil glands up to 0.5 mm diameter, densely villous-ciliolate along the margins, glabrous to puberulent on the back. Ray florets 5; corollas yellow or sometimes becoming reddish-tinged, 6–8 mm long, with oblong to ovate ligules 5–7 mm long and 2–3 mm wide, sparsely glandular-puberulent on the tube below. Disc florets 10–15; corollas yellow, 3.0–3.5 mm long, weakly bilabiate, with the narrow lobe 1–2 mm long, 2–3 times the length of the triangular glandless teeth on the broad lobe, glandular-puberulent on the tube. Achenes 3.5–4.0 mm long. Pappus of ray and disc similar, of 2–6 retrorsely-barbed awns 1–2 mm long. Chromosome number: $n = 12$. Flowering much of the year except during the driest summer months. Fig. 4.

Representative specimens: Sinaloa: 0.5 mi N of Topolobampo, 29 Dec 1963, *D. Flyr 71* (TEX); Topolobampo, 23 Mar 1910, *Rose, Standley, and Russell 13273* (US). Sonora: near Navojoa, 27 Oct 1939, *Gentry 4751* (ARIZ, MO, NY, UC); 28 m S of Hermosillo, 7 Sep 1971, *Keil and Canne 8602* (OS); 27 mi SE of Navojoa, 10 Sep 1971, *Keil and Canne 8734* (OS); Guaymas, 1887, *Palmer 143* (GH, NY, UC, US); Agiabampo, Oct 1890, *Palmer 759* (GH, MO, NY, UC, US); Torres, Jan-Mar 1902, *Purpus 416* (MO, UC, US); vicinity of Empalme, 11 Mar 1910, *Rose, Standley, and Russell 12632* (F, GH, MO, NY, US); 12 mi W of Hermosillo, 27 Aug 1941, *Wiggins and Rollins 122* (ARIZ, GH, LL, MO, NY, UC, US).

Pectis coulteri occurs from central Sonora to northern Sinaloa from

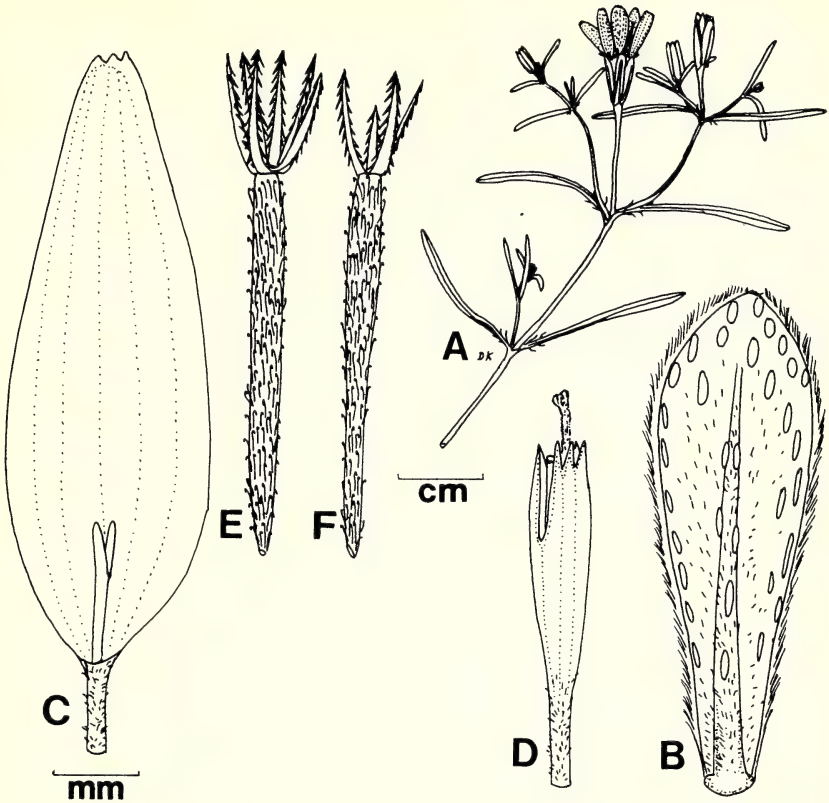

FIG. 4. *Pectis coulteri.* A, habit (*Keil and Canne 8728,* US); B, phyllary; C, ray corolla; D, disc corolla; E, ray achene; F, disc achene. B–F, same scale (*Keil and Canne 8730,* OS).

sea level to ca 500 m (fig. 1). Various authors (Gray, 1884; Fernald, 1897; Rydberg, 1916; Kittell, 1941; Kearney and Peebles, 1960; Shreve Wiggins, 1964) have also included southern Arizona within the range of *P. coulteri.* I believe that this inclusion is erroneous and that it represents the perpetuation of an old error. Two collections have apparently been the basis for listing *P. coulteri* in the flora of Arizona: (1) an early collection by Edward Palmer labeled "Arizona" without locality (GH); and (2) the type collection of *P. coulteri.*

The veracity of the label data on some of Edward Palmer's early collections from western North America has been challenged previously. McVaugh and Kearney (1943) list several instances of mislabeled specimens that Palmer supposedly had found in Arizona but actually had collected in other regions. This apparently is the situation in the case of *P. coulteri.* Palmer probably collected *P. coulteri* in Sonora rather than in Arizona during an 1869 trip from Tucson, Arizona, to Guaymas,

Sonora. Indeed, there is a collection of *P. coulteri* in US collected by Palmer in 1869 in Sonora with "Arizona" penciled on the label above "Sonora".

The locality for the type collection of *P. coulteri* is also confused. Thomas Coulter collected specimens of three different species of *Pectis* that were later described as new by Harvey and Gray (in Gray, 1849). All three, *P. coulteri, P. filipes,* and *P. papposa,* bear labels indicating that they had been collected in California (without localities or dates). Neither *P. coulteri* nor *P. filipes,* is known to grow in California, and this was recognized by Gray, himself (1884), who suggested that Coulter had collected the specimens in Arizona. Coville (1895) in documenting Coulter's 1832 trip to the mouth of the Gila River in Arizona added his support to the argument that Coulter had collected the type of *P. coulteri* in Arizona. In the same publication, however, Coville mentioned the case of *Berginia virgata* Benth. & Hook. (Acanthaceae), originally described from one of Coulter's "California" collections, later attributed to Arizona, and finally rediscovered in Sonora [and still known only from Mexico (Shreve and Wiggins, 1964)]. Keil (1973) has shown that a similar situation is true for *Pectis filipes,* for which the typical variety is wholly Mexican.

Coulter collected in Sonora in the vicinity of Hermosillo and Guaymas (Coville, 1895; McVaugh, 1943), areas where *P. coulteri, P. filipes,* and *P. papposa* are all common. It is in these regions that I believe he gathered the types for these species. Consequently, unless and until the occurrence of *Pectis coulteri* in Arizona can be documented with certainty, I feel that this species should be excluded from the known flora of Arizona.

The 1869 collection of *P. coulteri* by Edward Palmer (*s.n.,* US) that was mentioned above is morphologically peculiar. Unlike all other specimens of *P. coulteri* that I have examined, the single plant on this sheet has heads with 13 ray florets! Correlated with this feature are greater than usual numbers of disc florets and phyllaries much narrower than usual. I know of no other case in *Pectis* of a typically 5-rayed species having such an abnormality.

Acknowledgments

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REPRODUCTIVE BIOLOGY OF GOODYERA OBLONGIFOLIA (ORCHIDACEAE)

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Discovery of a large population of *Goodyera oblongifolia* Raf. prompted this investigation. Since some northern temperate orchids are known to have replaced or supplemented allogamy (cross-pollination) with autogamy (self-pollination) and asexual reproduction, the question arose as to what adaptations contributed to the success of the study population. Interrelations of vegetative propagation, self-compatibility, seed fertility, flower aggregation, nectar production, capsule development, pollination mechanisms, and pollinator distributions are considered.

Goodyera oblongifolia is distributed from Arizona to southeastern Alaska and east across Canada to the Great Lakes region. Disjunct populations occur in northeastern Mexico and in the vicinity of the St. Lawrence Seaway. Correll (1950) and Szczawinski (1969) reported *G. oblongifolia* abundant in certain localities and noted that the species spreads rapidly once established. In northern California, local populations of *G. oblongifolia,* growing in coniferous forests, consist of several to many colonies.

There are a few accounts of pollinators of the genus. Several authors observed *Bombus* pollinating *Goodyera repens* L. (Muller, 1873; Darwin, 1877; Hagerup, 1952) and Kipping (1971) observed *Bombus vosnesenskii* Rad. workers carrying pollinia and visiting *G. oblongifolia* in in the Sierra Nevada. Kipping also captured *B. mixtus* Cresson visiting the orchid but it bore no pollinia.

Autogamy and agamospermy occur in several northern temperate orchids. Hagerup (1952) found bud autogamy in several orchids of Denmark, including *G. repens.* Agamospermy, the production of seeds without the fusion of gametes, occurs in at least five genera of the Spiranthinae (Hagerup, 1945 and 1947; Swamy, 1946 and 1948; Maheshwari and Narayanaswami, 1953). Neither agamospermy nor autogamy has been reported in *Goodyera oblongifolia* (also Spiranthinae).

Materials and Methods

The study population consisted of several thousand plants located in a beach pine (*Pinus contorta* Doug. ex Loud.) climax forest community adjacent to coastal sand dunes, 3 km north of Manila, Humboldt County (T6N R1W Sec. 23 and 26), California. Ten 1 m^2 plots were staked for studies to determine percent capsule set and capsule maturation time, to record phenology of the population, and to evaluate floral density. Once or twice a week the number of buds, flowers, and capsules in each plot were recorded. Vouchers were deposited in HSC.

From outside the plots, two hundred plants, half flowering and half not flowering, were examined for number of new growths. In assessing vegetative propagation, only plants with a single, well developed basal rosette were used.

Self-compatibility and insect-exclusion experiments were designed. Five potted plants from the study population were placed in a screened room and tested for self-compatibility. Flowers were hand-pollinated by placing a pollinarium on the stigmatic surface. To determine if the species self-pollinated, I placed 12 potted plants in a cage that excluded all insects. Plants in this experiment were initially sprayed with a garden sulfur solution to rid them of insects.

Seed fertility was estimated for all capsules developed in the insect-exclusion and self-compatibility experiments, as well as for the capsules of ten naturally pollinated flowers collected from the study population. The technique used was much the same as that employed by Stort

(1973) and L. Thien (pers. comm., 1973). For each capsule, five slides were made and nine fields from each slide were viewed, 40×. A seed was considered fertile if it contained a developed embryo.

Pollinator effectiveness and pollination mechanics were assessed by observing pollinator behavior and by dissecting 341 variously aged fresh flowers and 128 withered flowers, all selected from the study population. Position of the column in relation to the lip (labellum), stickiness of the stigma and the viscidium, absence of pollinia, and presence of pollen on the stigma were noted for each fresh flower examined. Presence or absence of pollinia was also recorded for each withered flower.

Robbin Thorp (University of California, Davis) identified pollinators and deposited them in the UC Davis insect collection.

Results

The ten-week flowering period of the study population began 8 August and ended 18 October 1973. Each flower lasted approximately two weeks. Capsules matured in six to eight weeks, measured from the time the perianth withered to capsule dehiscence. Table 1 contains data from the ten plots.

Plants that were flowering usually produced more new rhizomatous growths than plants that were not flowering. Of plants in flower, 13 had no new growths, most had either one or two, and four plants had three. Of plants not in flower, 77 had no new growths, 22 had one, and one plant had two. The mean number of new growths was 1.74 for flowering plants and 0.46 for those not flowering.

The insect-exclusion experiment tested 111 flowers and 9.0 percent formed capsules; however, all fruits were parthenocarpic and from the same inflorescence. All hand-pollinated flowers in the self-compatibility

Table 1. Flower Density and Percent Capsule Set from a Population of Goodyera oblongifolia. Data are from 1 m^2 plots. See text for study population locality.

Plot	Plants flowering	Flowers	Flowers per inflorescence	Capsules	Capsule set (%)
1	8	133	16.6	70	52.6
2	11	104	9.4	70	67.3
3	7	75	10.7	28	37.3
4	15	207	13.8	105	50.7
5	18	202	11.2	27	13.3
6	17	197	11.6	104	52.7
7	15	208	13.8	120	57.6
8	9	98	10.9	22	22.7
9	18	218	12.1	124	56.8
10	9	118	13.1	52	44.0
Totals	127	1560	ave. = 12.3	722	ave. = 46.2

experiment developed fruit. Mean seed fertility was 52.7 percent (6,132 seeds from 14 capsules). Seed fertility of individual capsules varied from 2.1 to 98.8 percent. Examination of 4,874 seeds from ten fruits of naturally pollinated flowers showed 83.8 percent average seed fertility. Percent seed fertility for these capsules ranged from 62.7 to 96.6.

A few polyembryonic seeds were observed in capsules of high seed fertility. Polyembryony, not a rare phenomenon in orchids, is also known to occur in *G. tesselata* Lodd. and *G. pubescens* (Willd.) R. Br. (Leavitt, 1901). As defined by Wirth and Withner (1959), seeds with multiple embryos all derived from the same egg cell are polyembryonic. Although not proven by embryological studies, those few seeds were considered polyembryonic because the two embryos, and never more than two, were always partially fused. The low frequency of these seeds makes them insignificant to the reproductive biology of *G. oblongifolia*.

Queens of *Bombus occidentalis* Greene, laden with pollinia, were observed and captured while pollinating the orchid. Few bumblebees were seen visiting the population and were rarely observed on overcast days. Bees briefly visit several flowers per inflorescence, often working the lower flower first.

Goodyera oblongifolia is protandrous; pollen deposition is temporarily prevented by the close poximity of the column to the lip. When the flower opens, the column is horizontal relative to the labellum (fig. 1). In this position, the median groove of the lip forms a narrow tube with the elongate rostellum and viscidium. When a bee lands on the flower and probes for nectar, its galea contacts the sticky viscidium, which adheres to the bee's mouth parts so that the bee will leave the flower carrying pollinia. The narrow tube is large enough for the bee's probing proboscis but too small if the proboscis bears pollinia. A bee carrying pollinia is prevented from pollinating a young flower because the position of the column blocks access to the stigma. As the flower ages, the column becomes vertical and the viscidium, if still present, dries (fig. 1). If bees carrying pollinia visit such flowers, pollinia come in contact with the stigma and small chunks of pollen from the sectile pollinia are left on the stigma.

In 128 withered flowers, pollinia were missing in 44.5 percent. Pollen was found on 58.6 percent of stigmas in 181 wild fresh flowers with vertical columns. Capsules matured in 46.2 percent of the flowers from the ten plots studied (Table 1), notably less than the percentage of flowers pollinated. It is unlikely that the pollen found on the stigmas was foreign. In the vicinity of the *Goodyera* population, only two other orchids were flowering concurrently: *Piperia elegans* (Lindl.) Rydb. and *P. maritima* (Greene) Rydb. These two closely related piperias are probably adapted for moth pollination; pollinia are not likely to be transferred from them to *G. oblongifolia*.

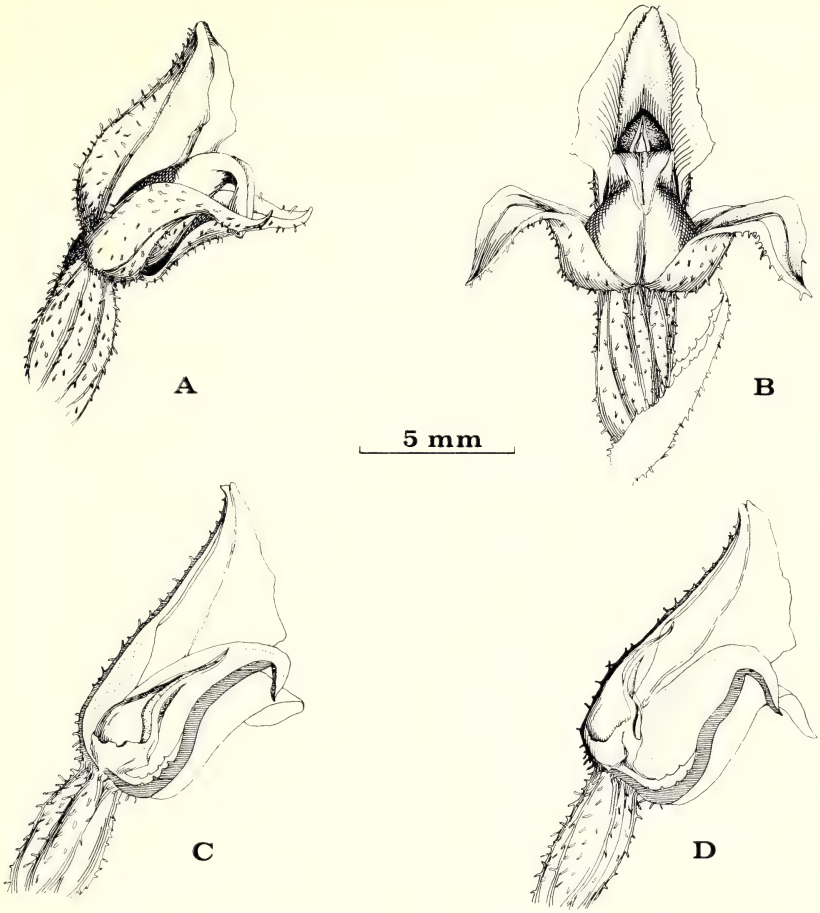

FIG. 1. Flowers of *Goodyera oblongifolia* Raf. A, side view; B, front view; C and D, perianth sectioned showing horizontal and vertical column positions.

DISCUSSION

Although parthenogenesis has been reported in related genera, I found no evidence for it in *G. oblongifolia*. Asexual reproduction, excluding vegetative propagation, probably does not occur in this species.

The capsule maturation period was short; the time interval between pollination and fertilization, although not determined, was correspondingly brief. Swamy (1949) suggested that a short time lapse between pollination and fertilization represents a primitive condition in the family. This may not necessarily be primitive but may have evolved secondarily in response to environmental conditions. The number of *G. oblongifolia* capsules that matured and dehisced was fewer than the

number of flowers pollinated. Whatever the mortality rate, it would be be higher if the capsules had to weather the winter.

Rhizomes of *Goodyera* produce leaves until terminated by an inflorescence (Stoutamire, 1974; Luer, 1975). For *G. oblongifolia,* a plant that flowers usually dies before the next flowering season. Loss of that member from the population is compensated since both flowering and nonflowering individuals reproduce vegetatively and a plant in flower usually develops more new growths than one not flowering. New growths become independent prior to senescence of the parent plant. This allows development of colonies exclusively by vegetative reproduction, which may be particularly important to very small populations where chances of pollination are diminished.

For potentially greater seed production, self-compatibility is advantageous for prolific clonal species (Estes and Brown, 1973; Estes and Thorp, 1974). Kipping (pers. comm., 1973) and I found *G. oblongifolia* to be self-compatible, although in my experiment, seed fertility (not determined by Kipping) dropped radically for some capsules. Nevertheless, mean fertility is high, indicative of self-compatibility. Chances of successful sexual reproduction in this species are not hindered by the combination of self-incompatibility and clonal populations.

Vegetative reproduction and self-compatibility are adaptive in *G. oblongifolia,* but they are also factors that can be detrimental to the genetic balance and plasticity of the species. Darwin (1877) and Gray (1862) suggested that inflorescences of *G. repens* are protandrous as a whole. Pollinia-carrying bees visit lower flowers first, pollinating them as they work up the inflorescence. Before leaving, the insect removes pollinia from the protandrous upper flowers; it then carries its new load to the next inflorescence. This was often the observed behavior of bees pollinating *G. oblongifolia.* The weakly protandrous inflorescence does not guarantee outcrosses nor do protandrous flowers because of the clonal population structure. The genetic effect of many pollinations is similar to autogamy; therefore much inbreeding occurs despite protandry. Nevertheless, outcrosses likely happen occasionally, thereby sporadically regenerating genetic variability in colonies of *G. oblongifolia.*

Results of the insect-exclusion experiment are negative: autogamy presumably does not occur.

The pollination mechanism described for *G. oblongifolia* is essentially the same as that discussed by Kipping (1971). Luer (1975) attributes this mechanism to North American representatives of *Spiranthes* and *Goodyera.* Contrary to my observations, Luer suggests that the mechanism of protandry involves a movement of the lip instead of the column.

Pollinators are likely to make repeated visits to flowers offering a food source. For example, a low percent capsule set was reported for orchids employing deception to lure pollinators (Mosquin, 1970; Thien and Marcks, 1972). In contrast, *G. oblongifolia* has a relatively high capsule set (Table 1). Nectar offered at the base of the saccate lip probably

encourages repeated pollinator visits.

As many as 30 flowers are aggregated on a raceme but racemes with 10–15 flowers are more common (Table 1). The clonal population structure clusters inflorescences so that the nectar producing flowers are grouped. The adaptive effects of flower aggregation, although relatively weak in *G. oblongifolia*, may be an increase in odor strength and visual stimulus and a localization of a food source.

Ranges of the three known pollinators, *Bombus mixtus, B. vosnesenskii,* and *B. occidentalis,* are sympatric with the western region of the orchid's distribution (Muesebeck et al., 1951). It is probable that several other species of *Bombus,* and maybe species of related genera, pollinate *G. oblongifolia* in western North America. Because this orchid is adapted to a group of commonly occurring pollinators and because orchid seeds are wind dispersed, the potential for range extension is great. Isolated populations in northeastern United States and adjacent Canada and in Nuevo Leon, Mexico, are possible realizations of that potential. However, Case (1964) believes disjunct populations in the Great Lakes Region are remnants of a once widespread distribution broken by glaciation. This reasonable suggestion does not refute the potentialities of successful long distance dispersal.

The short capsule maturation time minimizes capsule mortality during development. Self-compatibility, flower aggregation, nectar production, and adaptation to commonly occurring pollinators contribute to a greater number of pollinations. Protandry encourages outcrossing and so contributes to the maintenance of genetic variability. Adaptation to a widespread pollinator group and capabilities for vegetative propagation improve chances of successful establishment of new populations. These interactions are partially responsible for the success of the species.

Acknowledgments

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TAXONOMIC AND MORPHOLOGICAL OBSERVATIONS ON BOTRYCHIUM MULTIFIDUM (OPHIOGLOSSACEAE)

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Once upon a time, Clausen (1938) recognized five subspecies of *Botrychium multifidum* (Gmel.) Rupr. although he acknowledged that they grade insensibly into one another especially where their ranges are confluent. For example, the North American range of ssp. *silaifolium* (Presl) Clausen is from the Sierra Nevada to the Pacific Northwest and across

to northeastern North America and overlaps with that of ssp. *coulteri* (Underw.) Clausen and ssp. *californicum* (Underw.) Clausen in the Sierra Nevada and with ssp. *multifidum* (ssp. "*typicum*" of Clausen) in British Columbia and the southern portion of northeastern North America. In contrast, ssp. *robustum* (Rupr.) Clausen is restricted to Alaska and the ranges of ssp. *robustum,* ssp. *multifidum,* and ssp. *californicum* do not overlap. Apparently, the basis for establishment of these subspecies was their seemingly plurimodal distribution as revealed by herbarium data. However, because Clausen's (1938) monograph was based primarily upon herbarium specimens, representative collections of variation within populations were probably not obtained. In fact, the concept of the plurimodal distribution of these subspecies has been recently questioned by Hitchcock et al. (1969).

The Ophioglossaceae have been considered unique [with the exception of *Cheilanthes* spp. and *Pteris* spp. (Knobloch, 1965)] in the Filicopsida in that adult leaves do not exhibit circinate vernation but rather have erect (conduplicate) or a somewhat bent vernation. However, some morphological treatments (Milde, 1858, 1869; Campbell, 1911, 1940; Troll, 1939; and Bierhorst, 1971) figure young leaves of some of the larger species of *Botrychium* in which the vernation appears to be circinate. Thus, an investigation of buds with emerging leaves of large plants of *B. multifidum* would be appropriate in elucidating the concept of vernation in this taxon.

Baas-Becking (1921) indicated that the roots of *B. multifidum* may be contractile, a feature that would be unique in the ferns. However, because he had only one shoot bearing only a few roots, he was unable to investigate this fully. Further documentation of this and the aforementioned features of taxonomy and vernation are the themes of this study.

Materials and Methods

The following five Sierran populations of *B. multifidum* were observed, and collections of the subspecies circumscribed by Clausen (1938) as well as some intermediates have been deposited in the herbarium at the University of California at Davis: California, El Dorado Co., south of Lake Audrain, *Stevenson 365,* east side of Grass Lake at Luther Pass, *Stevenson 403–410*; Sierra Co., south side of Lower Sardine Lake, *Stevenson 367, 368*; Plumas Co., 0.8 km (0.5 mi) north of Grass Lake, *Stevenson 376–379*; Amador Co., north of Silver Lake near Kit Carson Lodge, *Stevenson 411–413.*

In addition, two smaller populations, one on the east side of Grass Lake, Plumas Co., and one at the west end of Lake Audrain were observed, but because of the paucity of individuals no collections were made.

Whole plants were killed and fixed in FPA. Some roots were removed at their point of attachment to the rhizome, embedded in Paraplast, and serially sectioned both longitudinally and transversely.

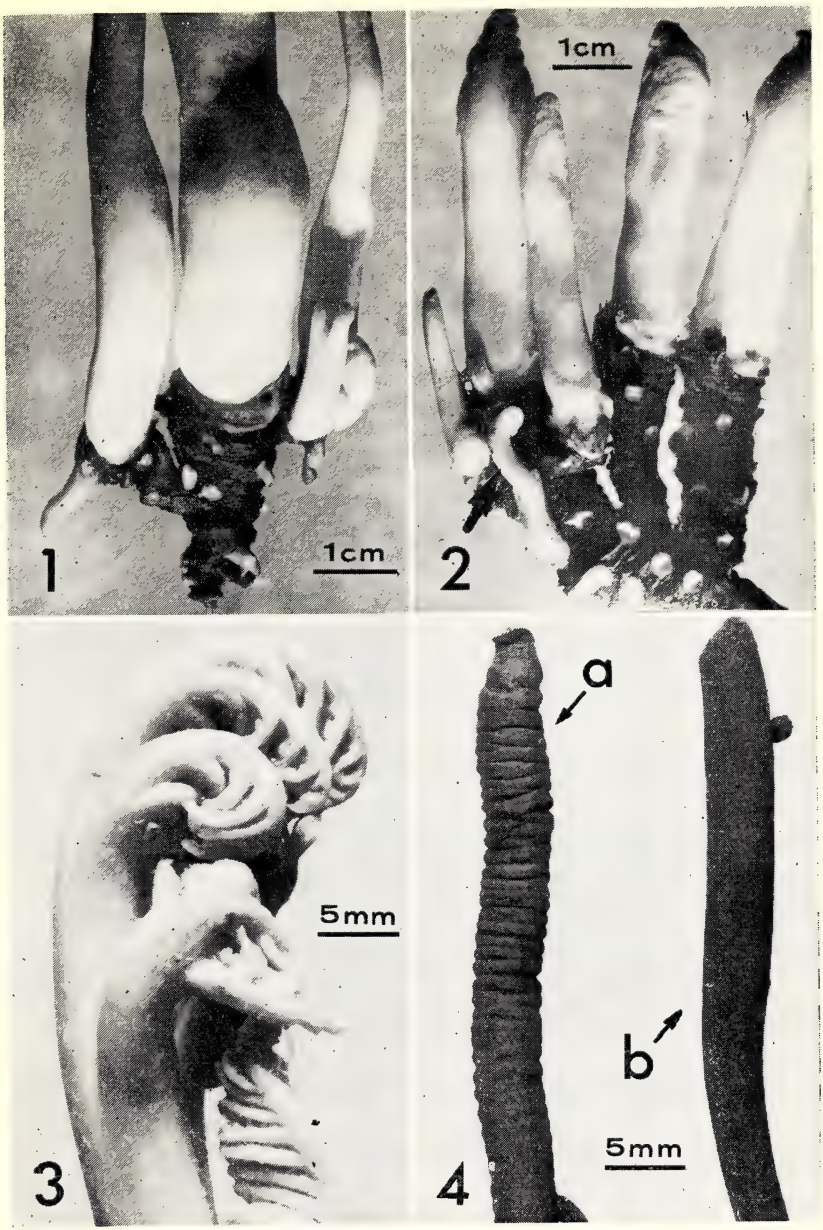
Observations and Discussion

Taxonomic considerations. The morphological characteristics of the five subspecies of *B. multifidum* as circumscribed by Clausen (1938) are at best vague except for individual plants representing extreme conditions. For example, in the large population of several hundred plants at Luther Pass, each individual usually was an intermediate. However, the few extreme individuals provided at least one representative of each of the subspecies. Thus, this population contained some individuals that could be referred to ssp. *robustum* and ssp. *multifidum*; these would be far outside their ranges as recorded by Clausen (1938). This was also true for all other populations under observation.

It could be argued that the intermediates could well represent hybrids of sympatrically growing subspecies. However, an intense search for gametophytes in each population proved fruitless. This search included taking soil samples from depths down to 45 cm and a careful examination of the soil particles was made with the aid of a hand lens both before and after sifting the soil with various soil sieves. Moreover, gametophytes of *B. multifidum* have never been observed except for one illustration by Milde (1858), which was interpretated by Clausen (1938), but not by Milde, as a gametophyte with an attached sporophyte. Thus, it seems that sexual reproduction in this species is very rare. Furthermore, most of the large plants are probably very old. Plants of this taxon usually produce only one leaf per year but occasionally may produce two in a growing season. Thus, a conservative estimate of the age of an individual plant can be made by counting the leaf scars on the rhizome and dividing by two. For example, large rhizomes that had rotted away at their basal ends were collected that had more than 200 leaf scars; these plants were therefore more than 100 years old. Even the relatively few small plants (some with leaves composed of only three undivided pinnae) had minimum ages of 15 to 30 years. The paucity of young plants further supports the theory of infrequent sexual reproduction.

What can appear in the field as several closely placed individual plants may represent one copiously branched individual (figs. 1, 2). In some cases two (fig. 7a, b) or even three branches of the same plant were referable to different subspecies as circumscribed by Clausen (1938). In conclusion then, recognition of subspecific taxa in *B. multifidum* is questionable on numerous grounds, the most convincing being the presence of more than one of the previously described subspecies as branches of the same individual!

Vernation. One of the unique features of leaves of the Ophioglossales is their putative lack of circinate vernation as opposed to its generally consistent occurrence in both the Marattiales and Filicales. Leaf vernation in the Ophioglossales has been described as erect in the smaller forms and bent in the larger forms. With respect to the latter, the two segments, sterile and fertile, are curved towards each other with the sterile segment over-arching the fertile segment (fig. 3). In *B. multifidum*

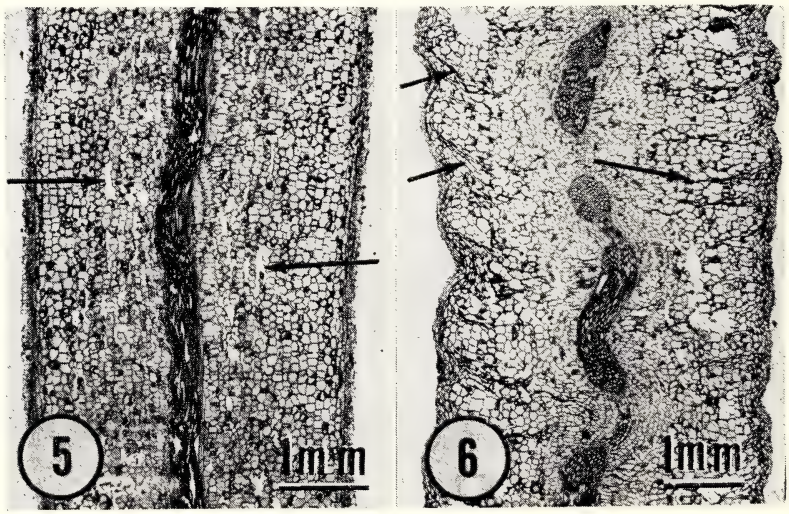


FIGS. 1–4. *Botrychium multifidum*. 1–2. Examples of highly branched individuals. Note circinate vernation of small leaf (arrow) in 2. 3. Large leaf with circinate vernation. 4. Older contracted root (a) and young uncontracted root (b).

(and throughout the Ophioglossales) each leaf primordium is enclosed in the stipular sheath of the next older leaf. The leaf and each of its sub-

sequent subdivisions grow by means of apical cells, as in the leaves of taxa placed in the Marattiales and Filicales. In vascular plants, growth of leaves by an apical cell is restricted to taxa with circinate vernation. Thus, it would not be inconsistent to expect circinate vernation of the large leaves of vigorously growing shoots of *B. multifidum*. An examination of emerging leaves of large plants of this species does indeed reveal circinate vernation of both fertile and sterile portions and their subdivisions (fig. 3). In fact, the degree of circination appears to increase with the increasing size of the mature leaves. In small plants bearing small leaves the leaves are merely bent or slightly circinate (fig. 2, arrow) as compared to larger leaves (fig. 3) of larger plants. Therefore, it seems reasonable to regard bent vernation of leaves of smaller species of *Botrychium* as diminutively circinate. Furthermore, occurrence of circinate vernation in the Ophioglossales makes their relationship with the Marattiales, and hence the Filicales, more tenable.

Contractile roots. The most obvious indication of contractile roots in *B. multifidum* is the wrinkled or corrugated appearance of the older roots (fig. 4a) as opposed to the smooth even appearance of young roots (fig. 4b). This wrinkled appearance usually extends from 2–4 cm along the root from its juncture with the rhizome (fig. 4a) and corresponds to the contracted portion of an individual root. The process of contraction was revealed by comparing serial sections of contracted roots with those of younger uncontracted roots. Lysigenous cavities form in the root cortex at somewhat regularly spaced intervals (fig. 5); then these cavities col-



FIGS. 5–6. Longisections of uncontracted and contracted roots of *Botrychium multifidum*. 5. Uncontracted root with developing lysigenous cavities (arrows) and a straight stele. 6. Contracted root with collapsed cavities (arrows) and undulating stele.

lapse (fig. 6) and the root contracts, resulting in the external wrinkled appearance. Also, the root stele, which is originally straight in longisection (fig. 5), becomes undulated or spiral so that only portions of it occur in any longisection (fig. 6). This method of root contraction is essentially the same as that reported for several species of *Oxalis* (Thoday, 1946; Davey, 1946).

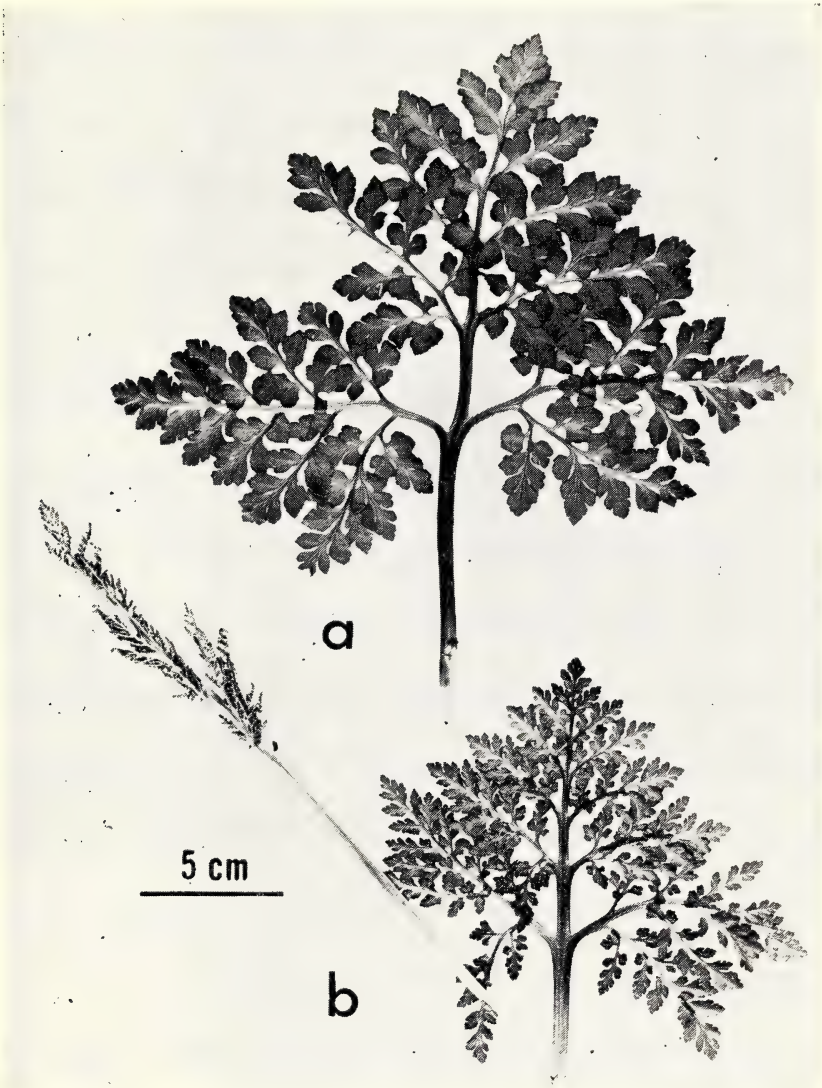


FIG. 7. A branched individual of *Botrychium multifidum* in which one shoot (a) has the characteristics of ssp. *californicum* and the other shoot (b) is intermediate between ssp. *coulteri* and ssp. *robustum*.

Occurrence of contractile roots in lower vascular plants seems to be limited to *B. multifidum*; however, there is some indication that they also occur in *B. dissectum*. Chamberlain (1920) described roots of this species as wrinkled and they are illustrated as such by Britton and Brown (1913). In addition, a cursory examination of herbarium specimens indicates that they are also present in *B. australe, B. jenmanii, B. alabamense,* and *B. underwoodianum*.

It is generally acknowledged that contractile roots either aid in anchoring plants in or on a substrate or in keeping them embedded in the soil. The latter appears to be the case in *B. multifidum* for the bud (the shoot apex and associated leaf primordia) is below the soil surface. As the shoot continues to grow and form new nodes, the vertical rhizome becomes longer as a result of the addition of the new growth increments. Eventually, the bud would arrive at the soil surface. However, the contractile roots that are produced at each node maintain the bud position below the surface. Thus, there is probably a balance established that maintains the bud at a more or less uniform distance beneath the soil surface.

Acknowledgments

I extend my gratitude to my son Michael Sean for locating the Lower Sardine Lake population of *B. multifidum* and to Drs. Ernest M. Gifford, Jr., Rudolf Schmid, and Arthur R. Spurr for their critical reading of the manuscript.

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A NEW VARIETY OF ERIOGONUM ERICIFOLIUM (POLYGONACEAE)

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While collecting towards a flora of the New York and Providence mountains of eastern San Bernardino County, California, a small series of populations of a very low-growing buckwheat was observed on a saddle on an exposed site west of Fourth of July Canyon in the New York Mountains. Early observations of the specimens by Robert F. Thorne revealed that they were unlike any other known buckwheat from California. Observations by the senior author indicated the taxon's similarity to *Eriogonum ericifolium* Torr. & Gray, one of the rarest species in the genus. As recently noted by Reveal (1971), one variety of this species (var. *ericifolium*) is known from only two collections: the type, (Coues and Palmer in 1865 near Fort Whipple, Arizona) and a collection by Mearns in 1887 near Forte Verde, Arizona, which is the type for a synonym, *E. mearnsii*. The more common phase of the species, var. *pulchrum* (Eastw.) Reveal, has been frequently collected, especially during this century, throughout its range in northern Arizona. However, var. *ericifolium* has escaped the attention of collectors in Arizona for eighty-five years. Careful examination of the plants from the New York Mountains collection has shown that they are distinct from var. *ericifolium* insofar as we know that taxon to date. As a result, we are proposing a new variety for this California population.

Eriogonum ericifolium Torr. & Gray var. **thornei** Reveal & Henrickson, var. nov. A var. *ericifolio* foliis 4–6 mm longis, villosis supra, petiolis 1–2 mm longis cum basibus 1–2(–3) mm longis, marginibus eglandulosis, involucris 1.5–2.0 mm longis, admodum glabris, floribus 1.5–2.0 mm longis, achaenis 2 mm longis differt.

Type: California, San Bernardino Co., about 64 airline km E of Baker in the New York Mountains 10.5 airline km SSW of Ivanpah along a trail to a ridge in the western portion of Fourth of July Canyon area, on exposed rocky granitic-quartzite ridge associated with *Pinus monophylla, Juniperus osteosperma, Yucca baccata, Opuntia,* and other shrubs at about 1810 m, near 35° 15′ N, 115° 25′ W, (center of the SW ¼ of sect. 35 of R 14 E, T 15 N), 20 Aug 1973, *Henrickson 12676.* Holotype, US! Isotypes, ARIZ! CSLA! MARY! NY! RSA! SD! TEX! UC!

The new variety is named for Dr. Robert F. Thorne of Rancho Santa Ana Botanic Garden, Claremont, California.

Variety *thornei* differs from var. *ericifolium* in having villous upper leaf blades (not glabrous) on petioles 1–3 mm (not 1 mm) long, and slightly longer petiole bases that are not glandular along the margin as in var. *ericifolium*. Involucres of var. *thornei* are merely 1.5–2.0 mm long, whereas those of var. *ericifolium* are 2.5 mm long. The tube of the involucre is pubescent without in the typical variant, but in the new variety only the very apex of the tube along the margin has hairs. The flowers of var. *thornei* range from 1.5–2.0 mm long, while those of var. *ericifolium* are larger, being 2.5–3.0 mm long. So far as we can ascertain, both variants have white tepals that are slightly dissimilar in shape, with the outer tepals being somewhat wider than the inner tepals. Although we have seen only immature achenes of both varieties, those of var. *thornei* are just slightly smaller than those of var. *ericifolium*.

Based on information available to us, it seems that var. *thornei* is a highly isolated population of *Eriogonum ericifolium*, restricted to this single location. It occurs at a slightly higher elevation than var. *ericifolium* and appears to be more woody. Until var. *ericifolium* can be rediscovered, the overall relationship between it and the new variant cannot be firmly established. Nevertheless, based on gross morphological similarities of these taxa, we seriously doubt that the addition of more material will greatly affect the placement of var. *thornei*.

The key to *Eriogonum* in Munz (1968) can be altered after AA, B, CC, DD, E, FF, G, H, II, J, KK to read:

L. Infl. a compact terminal cyme; invols. tomentose or glabrous.
  M. Plants low spreading subshrubs in montane places to shrubs at lower elevations, up to 10 dm high; lvs. not revolute, or if so, then plants distinctly shrubby, the blades (3)10–30 mm long; common. 74. *E. microthecum*
  MM. Plants low, compact subshrubs of desert places, less than 2 dm high; lvs. revolute, the blades 4–6 mm long; New York Mts. 74a. *E. ericifolium* var. *thornei*

74a. E. ERICIFOLIUM Torr. & Gray var. THORNEI Reveal & Henrickson. Low spreading pulvinate subshrubs 0.4–1.0(–1.5) dm high, 1.0–3.5 (–4.4) dm across, from low woody caudices; lvs. linear, 4–6 mm long, white-tomentose below, finely villous and green above, revolute, narrowing gradually to a petiole 1–3 mm long; flowering stems herbaceous, leafy nearly throughout their length, 3–5 cm long, thinly pubescent; infl. compact, up to 2 cm long; invols. turbinate, 1.5–2.0 mm long, glabrous except for the apex, the 5 teeth acute, sessile or short peduncled; calyx white, becoming pinkish, 1.5–2.0 mm long, the outer segms. obovate with subcordate bases, the inner narrower, oblong, glabrous; aks. narrow, 2 mm long. Known only from W Fourth of July Canyon, New York Mts., 1810 m (5950 ft) elev., San Bernardino Co. July–Aug.

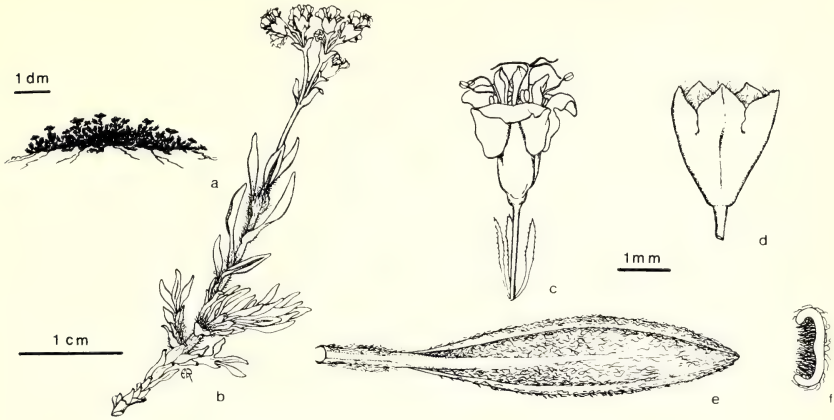

FIG 1. *Eriogonum ericifolium* var. *thornei*. a, habit. b, flowering shoot. c, flower with bractlets. d, involucre. e, leaf showing lower surface and clasping petiole base. f, cross section of leaf showing revolute margins. Magnification of c–f shown by mm scale.

The new taxon is very restricted in distribution, occurring only along 0.6 km of a northwest-southeast oriented ridge from 1871–1804 m (6140–5920 ft), and occupies a maximum area of less than one hectare. Although var. *thornei* is restricted to this ridge, it is notably abundant, and the area is marked by a conspicuous decrease in density and diversity of vegetation, as indicated in Table 1. Only *Pinus monophylla* shows little change in density on and around the site. However, the pinyons occurring with the new taxon were notably smaller (0.2–2.2 m high, average: 0.65 m) than those on adjacent slopes and ridges (0.2–5.6 m high, average: 1.3 m). The new variety often occurs in pure stands or mixed with *Eriogonum wrightii* var. *wrightii, Bouteloua gracilis, Allium nevadensis* var. *cristatum, Menodora scabra, Coryphantha vivipara* var. *rosea, Hymenopappus filifolius* var. *eriopodus* as well as species of *Astragalus, Cymopteris,* and *Caulanthus*, all of which also continued onto adjacent areas. Furthermore, the new taxon appears particularly well adapted to its habitat, as young plants are common especially in disturbed places as along a roadcut that traverses the site.

The greatly restricted occurrence of var. *thornei,* its local abundance, and the distinct change in vegetation around the site indicate that some edaphic factors may be involved in its limited distribution. Soil on the site is a rocky, sandy loam composed of a weathered quartz monzonite with fragments of vein quartz. Initial analysis of a soil sample collected under plants of the new taxon revealed a particularly high concentration of copper (312 ppm). Additional samples collected from two outlying populations of var. *thornei* had 236 and 176 ppm copper. One other site directly contiguous with that containing the variety, but covered with a nearly pure stand of *E. wrightii* var. *wrightii,* contained 138 ppm copper.

TABLE 1. DENSITY IN NUMBER PER HECTARE OF MAJOR TREES AND SHRUBS OVER THE SITE WITH (COLUMN A) AND ON ADJACENT AREAS WITHOUT (COLUMN B) ERIOGONUM ERICIFOLIUM VAR. THORNEI. Measurements of *E. ericifolium* var. *thornei* and *E. wrightii* var. *wrightii* are based on sample of 67.3 m^2 with 61 × 61 cm (2 × 2 ft) quadrats. Density of other species is based on ten 0.004 ha (0.01 acre) samples. The density of *E. wrightii* var. *wrightii* was not measured (nm) outside the area occupied by var. *thornei*.

	A	B
Eriogonum ericifolium var. *thornei* Reveal & Henrickson	89,000	0
Eriogonum wrightii Torr. ex Benth. in DC. var. *wrightii*	61,000	nm
Pinus monophylla Torr. & Frem.	514	524
Echinocereus triglochidiatus var. *mohavensis* (Englem. & Bigel.) Benson	820	514
Opuntia erinacea var. *ursina* (Weber) Parish	1057	1877
Opuntia phaecantha cf. var. *major* Engelm.	30	326
Yucca baccata Torr. var. *baccata*	128	622
Juniperus osteosperma (Torr.) Little	....	217
Quercus turbinella Greene	....	296
Haplopappus linearifolium DC.	....	731
Gutierrezia microcephala (DC.) Gray	....	1491
Purshia glandulosa Curran	....	395
Ephedra viridis Cov.	....	119
Opuntia acanthocarpa Engelm. & Bigel.	....	30

Other immediately adjacent sites where the new variety did not occur had only 78, 19, and 4 ppm copper. The site furthermore contains several open pit diggings that showed the presence of shallow deposits of malachite and azurite. Thus, we believe, the distribution of var. *thornei* is strongly influenced by the distribution of copper bearing soils at this particular location. Fortunately the concentration of copper on the site is so low that commercial exploitation would not be feasible.

That copper may affect the distribution of plants is well known. Cannon (1971) discussed many facets of plant-soil relationships and listed species that have been noted as restricted to particular mineralized sites. This restriction, she noted, most commonly involves a tolerance of a particular compound that inhibits growth of other plants. She listed several species of *Eriogonum* that in some areas serve as indicators of gypsum, serpentine, and silver deposits. While this is the first reported incidence of a buckwheat showing restriction to a copper containing soil, similar edaphic relationships probably occur elsewhere in the genus and are important in determining the distribution of the numerous highly endemic species of *Eriogonum*.

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and Sons, Riverside, California. Barry Prigge and Christopher Davidson assisted in quantitative studies. Frances Runyan provided the illustration.

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PRIMARY SUCCESSION ON GRANITE OUTCROPS IN THE MONTANE SOUTHERN SIERRA NEVADA

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Although primary succession has been widely studied, little attention has been given to its occurrence in the mountains of the western United States, despite the extensive distribution of rock outcrops. On the west slope of the Sierra Nevada, 29 percent of the total area above 1,543 m (5,000 ft) consists of rock or bare ground surfaces (Richards, 1959). This paper reports on general patterns of primary succession present on granite outcrops in the montane zone of the southern Sierra Nevada of California, including colonization by both cryptogams and vascular plants.

Much of the ecological literature on primary succession on rock surfaces (e.g., Cooper, 1913; Oosting and Anderson, 1937; Lawrence, 1958) have implied that primary succession progresses linearly from colonization by cryptogams, through herbaceous and shrub communities to an eventual climax forest community. Each later stage is dependent on physical and biotic changes brought about by the earlier stage. Recent studies in Hawaii on lava rock, however, have shown that a different progression can occur (Atkinson, 1970). *Metrosideros collina* (ohia) is the dominant climax forest species on incipiently weathered lava and is also one of the first colonizers on sterile outcrops. While cryptogamic communities may become established more rapidly, they have little significance in the establishment of *Metrosideros* seedlings within crevices on the lava outcrops.

Primary succession on granite outcrops in the montane southern Sierra Nevada shows a pattern similar to that described for *Metrosideros* in Hawaii. Climax woody species appear early in the successful development of the outcrops, with little influence of cryptogamic or herbaceous com-

munities. While lichens and bryophytes comprise the earliest colonizers on granite outcrops, succession on these outcrops is primarily a function of physiographic weathering leading to the formation of fracture lines suitable for colonization by woody plants. Although environmental modifications brought about by bryophyte communities may lead to outcrop colonization by vascular plants, this situation is rarely important in the overall succession toward climax communities. In describing the general nature and patterns of primary colonization and succession as they occur on granite outcrops in the montane zone of the southern Sierra Nevada, this paper includes a broad discussion of both the nature of early outcrop colonization by lichens and mosses and the relationship of vascular plant colonization to crevice formation and soil development on outcrop surfaces.

Materials and Methods

A series of granite outcrops between 1900 and 2100 m was studied extensively in Sequoia National Park and Sequoia National Forest. Detailed analysis and physiological measurements were carried out on a southwest-facing outcrop 0.5 km west of Crescent Meadow, Giant Forest, Sequoia National Park.

Analyses of soil chemistry were made by the Soil Testing Division, North Carolina State University, Raleigh. Methods of determination were as follows: pH-glass electrode; organic matter—H_2SO_4-$Na_2Cr_2O_7$; and Ca, P, K, NH—HC1-H_2SO_4 extract. Water potential measurements were made with a Scholander-type pressure bomb. Details of the methods of pressure bomb measurements have been previously described (Rundel, 1972). Growth increment measurements of tree cores were made with a dissecting microscope utilizing a dendrometer constructed from a threaded mounting stage and Ames dial micrometer.

I thank William A. Weber for assistance in the identification of lichen species and Richard Zander for identification of bryophytes. Lichen nomenclature follows that of Hale and Culberson (1970), bryophytes that of Crum et al. (1973). Vascular plant nomenclature follows Munz (1959).

General Pattern of Succession

General patterns of outcrop succession are shown in Figure 1. Smooth granite outcrops provide a poor substrate for vascular plant growth; therefore primary colonizers are restricted to lichens and bryophytes. Although environmental modifications brought about by certain bryophytes may lead to outcrop colonization by vascular plants, this situation is unimportant in the overall succession toward climax communities. Only rarely are vascular plants able to colonize an outcrop before physiographic weathering has produced suitable habitats in the form of fracture lines. A variety of herbaceous perennials and woody species are able to colonize crevices with sand accumulation and adequate moisture

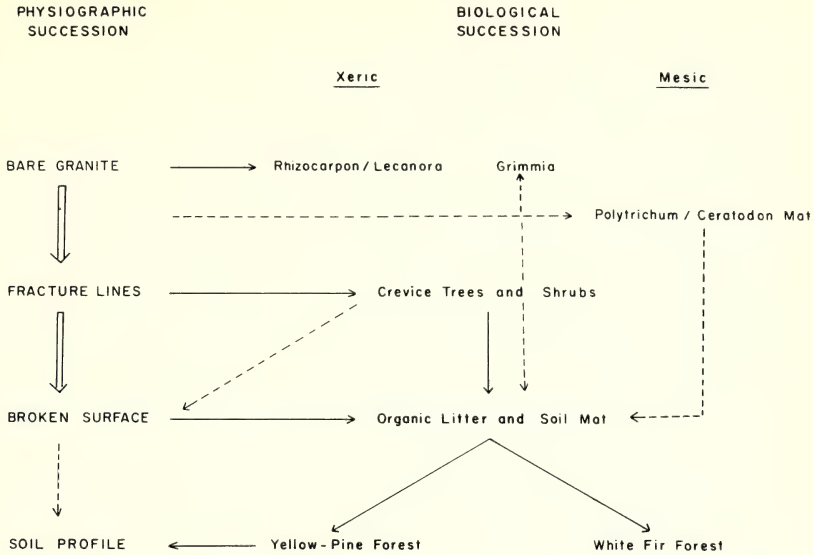

FIG. 1. Primary succession on granite outcrops in the montane southern Sierra Nevada.

conditions. Even individuals of climax coniferous tree species may become colonizers at this stage.

For biological succession to progress from crevice plant colonizers to a climax coniferous forest, it is necessary to develop an organic soil mat. There are two means by which such soil mats may develop. Without question the most important process by which soil mat formation takes place is the in situ formation of soils on broken outcrop surfaces in the most developed stage of physiographic succession. With repeated fracturing of horizontal granite outcrops, aided by winter freeze-thaw cycles, the surface of the outcrop is eventually broken into an irregular accumulation of angular rocks and boulders. The time necessary to produce such a broken surface by physiographic succession is extremely variable, depending on the structural relationships of individual outcrops. Once a broken outcrop surface exists, soil formation can proceed at a steadily accelerating pace. Of lesser importance overall is soil mat formation from litter accumulation around the bases of colonizing trees and shrubs in crevice habitats. Under stable conditions, an increasingly well-developed organic soil mat expands outward as litter fall continues.

BIOLOGICAL SUCCESSION

Colonization by Lichens. Two species of crustose lichens, *Rhizocarpon bolanderi* and *Lecanora gibbosa,* overwhelmingly dominate the earliest stages of succession on montane granite outcrops in the southern Sierra

Nevada. The majority of the exposed granite surfaces of the outcrops are covered by these two species, in particular the former. Only in areas of rapidly exfoliating rock surface or in channels subject to the abrasive action of runoff from snow melt and precipitation are these species absent.

Few other species of lichens occur with any regularity on the exposed horizontal surfaces of these outcrops. *Dermatocarpon miniatum* and *Candelariella* sp. occur irregularly on the outcrops but never with large coverage. The great majority of saxicolous species on the outcrops occur on sites with reduced levels of solar radiation, such as vertical rock faces or on the sides of loose granite boulders. *Rhizocarpon geographicum, Lecidea* spp., *Umbilicaria phaea,* and *Parmelia conspersa* are typical associates in these habitats.

Colonization by Bryophytes. Despite the abundance of crustose lichens on the granite outcrops, these species contribute little if any to the succession toward more advanced plant communities. Another early colonizer on the outcrop surface, *Grimmia unicolor,* is far more important in biological succession.

Conditions for the establishment of *Grimmia unicolor* on the outcrops are ideal during the late spring in the Sierra Nevada. The necessary conditions for successful vegetative establishment of *Grimmia laevigata* on granite outcrops were described by Keever (1957) as follows: 1) wetting of a fragment of a *Grimmia* gametophyte by heavy dew or rain every 4–5 days for at least 2–3 weeks; 2) cloudy, cool but not freezing weather; and 3) subsequent dry, sunny weather. Conditions present on granite outcrops during spring snow melt in the Sierra Nevada provide this sequence of events. Vegetative growth is accomplished through the spread of protonema. Once established, these protonema are extremely drought resistent, and they may survive a month or more without any addition of water. Mature gametophytes of *Grimmia laevigata* are known to remain viable for ten years or more in herbaria (Keever, 1957).

The distribution of *Grimmia unicolor* on the granite outcrops is strongly related to the microtopography of the outcrop. In most instances the occurrence of *Grimmia* is correlated with minute rough places in the granite surface where the gametophytes have been able to form a strong attachment. *Grimmia* is most common on the granite outcrops along the margins of drainage channels. *Grimmia* is absent from the bottoms of these channels, apparently kept out by the abrasive action of water and sand during spring runoff; it is almost always present along the margins of these channels. The microtopography of channel margins provides a roughened surface to trap fragments of *Grimmia,* which are kept moist in the early stages of their establishment by water from spring snow melt moving along the drainage channel.

Although small *Grimmia* mats may trap significant amounts of weathered granite soil (up to 10 mm in depth), the irregular presence of these small mats makes them of minimal importance in biological succession

leading to communities of vascular plants. Rarely, *Grimmia* is found along the margins of organic litter mats, indicating that *Grimmia* is of some value in extending margins of mats. Establishment of these *Grimmia* populations, however, undoubtedly postdates the formation of the litter mat, as indicated by restriction of these populations to the downslope margins of mats. Seepage of water trapped by mats provides ideal conditions for establishment of *Grimmia*.

Seepage zones and channels on granite outcrops commonly produce a more mesic development of bryophyte colonization. The most widespread community of this seepage zone succession is the *Polytrichum juniperinum-Ceratodon purpureus* mat. Small to moderately-sized mats of discontinuous distribution form along areas where seepage flows during periods of precipitation or snow melt.

Small, discontinuous *Polytrichum-Ceratodon* mats are common in areas of shallow soil accumulation on broken granite surfaces. In almost all cases, these mats are associated with what appear to be runoff channels, collecting water in times of precipitation from other parts of the outcrop. Where drainage channels are well-defined, the mats may be restricted to margins of channels. Generally, the center of these well-defined channels are bare of soil or any lichens or bryophytes. In certain instances, however, thick mats of *Rhacomitrium fasciculare* may cover the smooth surface of the channel. Soil accumulation in such mats reaches 5 cm. Major drainage channels along outcrops often show a gradation from thick mats of *Rhacomitrium fasciculare* in the center of the channel to an irregular band of *Polytrichum-Ceratodon* mat along the inner margin of the channel. *Grimmia unicolor* occurs along the outer margins of these channels.

On relatively steep granite slopes of 20–30° or more, pure mats of *Ceratodon purpureus* are common where springs or late snow melt provide a continuously wet rock surface well into the summer months. Soil accumulation reaches 5 cm or more within these mats. If water supply is adequate, the mats will support growth of a variety of annual vascular plants. Mats of *Bryum* or *Tortula ruralis* in similar situations may also support herb growth, typically *Linanthus montanus*. Such occurrences of herbaceous species growing from the soil accumulated within moss mats, however, are rare.

Although a number of species of bryophytes are common primary colonizers on granite outcrops in the southern Sierra Nevada, it is rare that they play a significant role in biological succession leading to establishment of vascular plant species on the outcrops. In no instance has primary succession by *Grimmia bicolor* been observed to lead to establishment of higher plants. Where vegetation mats have been formed as a result of other conditions, as described later in this paper, *Grimmia* may occasionally play a small part in increasing the outer margin of an outcrop by accumulation of soil debris. Thick mats of moss in seepage zones may build soil mats to 5 cm in depth but this soil accumulation

rarely, if ever, leads to establishment of a more advanced stage of succession.

Crevice Succession. As physiographic succession proceeds from bare granite to the formation of fracture lines across the surface, vascular plants are able to colonize outcrops. On the majority of outcrops, fracture line crevices are a prominent feature. Typically these fracture lines average 2–5 cm in width and may extend for 20 m or more across the outcrop. Wind-blown sands and organic matter collect within these crevices.

On most montane outcrops in the southern Sierra Nevada, *Zauschneria californica* ssp. *latifolia* is the primary vascular plant colonizer of the crevice habitat. Even along fracture lines where soil accumulation within crevices is essentially absent, *Zauschneria* is commonly found. Often it is the only vascular plant present over large portions of outcrops. Second in importance is *Lomatium torreyi,* endemic to the central and southern Sierra Nevada. Although not as frequent as *Zauschneria, L. torreyi* often shows greater densities on individual outcrops. Both species are characterized by thick, woody taproots, possibly a morphological adaptation for water and carbohydrate storage. Four other species are also characteristic of this crevice community. *Calyptridium umbellatum,* while not restricted to this habitat, is common along fracture lines on outcrops. *Hieracium horridum, Streptanthus tortuosus,* and *Eriogonum wrightii* var. *subscaposum* may be locally important, but none of these species was present on a majority of outcrops studied.

Crevices beneath ledges or shaded by large boulders often include one or more species of ferns: *Pellaea bridgesii, Onychium densum,* and *Cheilanthes gracillima. Zauschneria californica* var. *latifolia* is again present. The moisture relations of these sites must be more favorable than along more exposed fracture lines, for these same species occur in rocky areas where seepage from snowmelt and spring rains continues into summer.

Establishment of Woody Plants. The establishment of woody plants is the most significant stage in colonization of granite outcrops leading to the development of soil cover. During years of favorable conditions, seeds of a number of tree and shrub species germinate and establish seedlings in soil within crevices. *Pinus jeffreyi, Libocedrus decurrens,* and *Arctostaphylos patula* occur frequently as primary colonizers on outcrops studied. Less frequently, a number of other trees and shrubs may act as primary colonizers. These include (in order of decreasing frequency of occurrence) *Pinus ponderosa* (below 1800 m), *Quercus kelloggii, Quercus chrysolepis, Arctostaphylos viscida* (below 1800 m), *Abies concolor,* and *Ceanothus cordulatus.* There is no evidence that the establishment of any of these species requires any previous biological succession on an outcrop. Given minimal levels of available moisture, windblown sand and trapped soil particles provide sufficient conditions for seedling establishment. A number of characteristically mesic species are also occasion-

ally found as primary colonizers, including *Corylus rostrata, Rubus parviflorus,* and *Sequoiadendron giganteum.*

The typical pattern of establishment of woody colonizers in crevice microhabitats consists of a period of years of slow growth while root systems become established, followed by more rapid growth when the root system is able to tap a reliable source of underground water. This pattern is illustrated in Figure 2 for two *Libocedrus decurrens* growing in crevice habitats on an outcrop near Crescent Meadow (Sequoia National Park). Both of these trees are stunted. Tree 1 shows a slow but increasing annual increment of growth over its first 25 years. From that point, it has shown a mean annual growth increment of about 1.5 mm, oscillating in relation to annual precipitation. Tree 2 likewise showed a slow relative growth rate for its first 25 years, followed by a rapid increase to a mean annual growth increment of approximately 2.5 mm.

The observed growth response of these two trees correlated well with patterns of water stress measured during the summer of 1968. Tree 1 with a mean annual growth increment of 1.0 to 1.5 mm had a maximum midday xylem pressure potential (shaded branch) of −27.2 bars in midsummer. It produced no cones in 1968. Tree 2, with a sparse cone crop, had a lower maximum stress of −25.7 bars. Individuals of *L. decurrens* with similar diameters (dbh) but normal height and heavy cone crop, growing on shallow soils nearby had a maximum stress of −18 bars. This maximum stress occurred relatively late in summer, allowing a much longer growing season than for the two outcrop trees. Restricted growing seasons for the outcrop trees is apparently reflected in a lack of available carbohydrate reserves for normal height growth and production of cone crops.

Formation of Soil Mats. Although vascular plants are first able to colonize granite outcrops during the fracture line stage of physiographic succession, few species successfully develop in these specialized crevice habitats. Diversity of the outcrop community can increase only following formation of a suitable soil substrate for germination and establishment of a larger flora of annual and perennial species. Such a soil substrate may develop either by the action of physiographic succession on the outcrop or by biological succession acting through accumulation of litter under crevice shrubs and trees.

In the first stages of physiographic succession on broken outcrop surfaces, vascular plants occur infrequently. Jumbled, angular rocks dominate the outcrop surface. Sands and gravels are primarily restricted to crevices, although wind-blown sediments may collect behind sheltered rocks or in vernal pools on the outcrop. Vascular plants are limited to crevice habitats, as previously described. As physiographic succession continues, accumulations of granite sand develop, forming an irregular layer 1 cm or more in depth. Little or no organic matter is present and vascular plants are rare or absent. The dominant perennials *Calyptridium umbellatum, Streptanthus tortuosus, Eriogonum wrightii* var. *subscapo-*

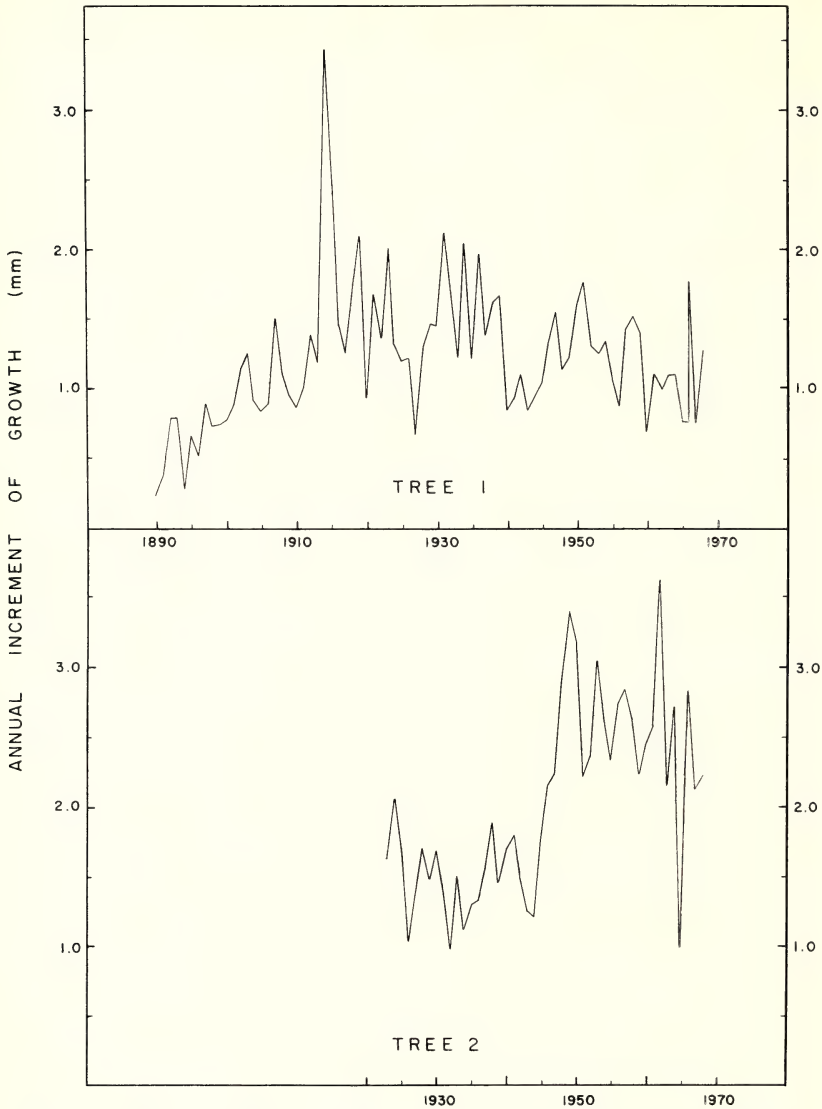

FIG. 2. Annual increment of growth for two *Libocedrus decurrens* growing in crevice habitats on a granite outcrop at 2040 m near Crescent Meadow (Giant Forest), Sequoia National Park.

sum, and *Lomatium torreyi* are joined by *Eriogonum nudum, Polytrichum juniperinum,* and *Ceratodon purpureus.* Basal rosettes of *Calyptridium umbellatum* and *Eriogonum nudum* are particularly frequent.

Diversity of outcrop communities increases rapidly as continued weathing processes produce relatively continuous granitic sands, richer in

finer sands, particles, silt, and organic matter. Outcrop surfaces with 2–5 cm of granitic soil are characterized by relatively rich carpets of spring annuals.

Linanthus montanus may carpet almost every square centimeter of the thin soil on outcrops. Locally, *Phacelia orogenes* and *Eriogonum spergulinum* may be abundant. A number of perennial species are also of importance: *Calyptridium umbellatum, Pteryxia terebinthina* var. *californica, Lotus nevadensis,* and *Perideridia gairdneri.* With the formation of distinctive soil profiles, 5–15 cm or more in depth and rich in organic matter, these species are replaced or overshadowed by a group of herbaceous species characteristic of xerophytic communities within yellow pine forests, e.g., *Pedicularis semibarbatus, Viola purpurea, Allophyllum integrifolium, Gayophytum nuttallii, Horkelia tridentata, Cryptantha affine,* and *Stipa* spp. These species are also common in open areas in the *Pinus ponderosa* (*P. jeffreyi*)/*Arctostaphylos* community on more developed sites. Climax species of trees and shrubs begin to colonize outcrop surfaces at this stage without reliance on crevices.

Biologically induced succession through the accumulation of organic litter in mats beneath crevice trees and shrubs on outcrops may also lead to development of significant soil substrates on outcrops. Organic debris is the most important element in early development of these litter mats. Granitic sands, important in the physiographic formation of outcrop soils, do not build up to significant depths until an organic substrate accumulates to trap them. Litter mats 5–10 cm in depth are common beneath isolated, crevice-growing individuals of *Arctostaphylos patula* and *Pinus jeffreyi.* Where hollows on the outcrop shelter the rock surface beneath crevice trees and shrubs, the accumulation of organic debris (and trapped inorganic sands) may be considerably greater. As organic litter accumulation exceeds a few centimeters in depth, herbaceous species colonize the soil mat. In almost all cases, these species are identical with those typical of the latter two stages.

Although chemical changes associated with soil development on granite outcrops have not been studied in detail, some idea of the changes involved can be seen in results of a transect made across an outcrop near Crescent Meadow, where soils were sampled at varying stages of successional development from primary moss colonizers to mature forest. Soil samples were collected from debris beneath thalli of *Grimmia unicolor,* the primary bryophyte colonizer on bare outcrop surfaces. A second series of samples was collected beneath mats of *Polytrichum juniperinum,* where 1–2 cm or more of soil was often present. Finally, samples were collected at two sites supporting coniferous trees: shallow soil mats (20–50 cm) at the outcrop edge with *Abies concolor* and *Libocedrus decurrens*; deeper soils (40–90 cm) at the margin of a grove of *Sequoiadendron giganteum.* Changes in soil chemistry determined along this gradient are shown in Figure 3.

Soil pH changed steadily with succession from 4.4 beneath *Grimmia*

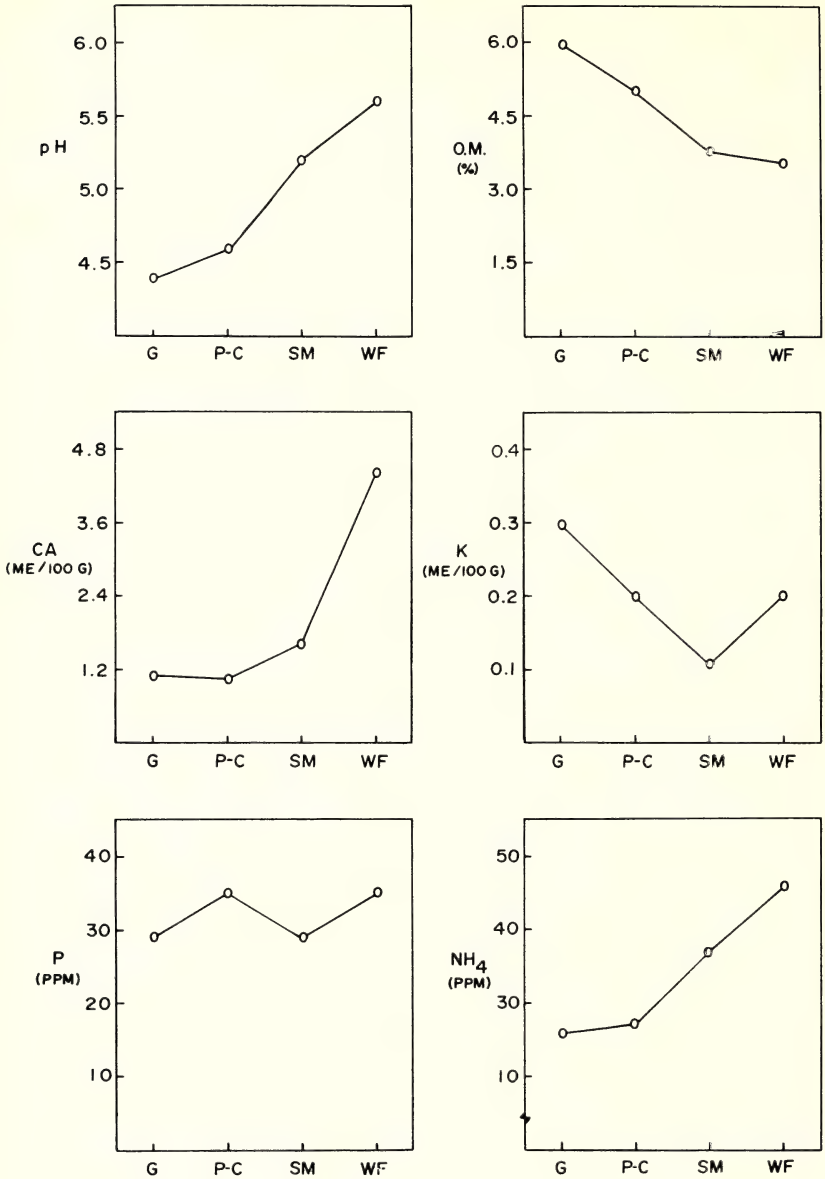

FIG. 3. Gradient of soil chemical characteristics (pH, organic matter, Ca, K, P, NH_4) across a granite outcrop at 2040 m near Crescent Meadow (Giant Forest), Sequoia National Park. G = *Grimmia* stage, P-C = *Polytrichum-Ceratodon* mat, SM = soil mat at edge of white fir forest (20–50 cm soil profile), WF = white fir forest with 40–90 cm soil profile.

to 5.6 in soils associated with *Sequoiadrendon*. Organic matter content, highest beneath the moss mats due to litter from the thalli above, was relatively consistent between 3.5 and 3.6 percent under the coniferous canopy. This low level indicates the extremely slow accumulation of organic matter in these soils. Both Ca and NH_4 show steady increases with greater soil development, while K appears to become slightly reduced in concentration. Major changes in P concentration were not observed.

Climax Vegetation. Climax vegetation in montane southern Sierra Nevada consists of a coniferous forest of variable composition. Differential fire history has produced a mosaic of forest stands differing in structure and species importance. The role of fire in successional sequences in the Sierra Nevada is beyond the scope of this paper. Many papers discuss this subject in detail (Show and Kotok, 1924; Rundel, 1971; Vankat, 1970; Kilgore, 1973).

Mesic facies of mature forest communties in the study area are strongly dominated by *Abies concolor*. *Pinus lambertiana* is a constant associate, and *Libocedrus decurrens* may be important, particularly below 1880 m. *Sequoiadendron giganteum* is an important associate locally in areas with abundant ground water. Characteristic understory species include *Corylus rostrata, Cornus nuttallii, Pteridium aquilinum* var. *lanuginosum,* and *Rubus parviflorus*. Xeric facies of mature forest communities can best be designated as yellow pine forest. The dominant tree species are *Pinus jeffreyi* and *P. ponderosa,* with *Libocedrus decurrens* and *Quercus kelloggii* as regular associates. Characteristic understory species are *Chamaebatia foliolosa, Arctostaphylos patula, A. viscida* (below 1800 m), *Ceanothus integerrimus,* and *Ribes roezlii.*

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PROSOPIS PALMERI: A RELICT OF AN ANCIENT NORTH AMERICAN COLONIZATION

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Baja California has long been recognized as the home of many endemic and often bizarre plant taxa (Shreve and Wiggins, 1964; Humphrey, 1970). Even the genus *Prosopis* (Leguminosae, Mimosoideae), usually thought of in terms of commonplace mesquites and screwbeans, has a singular representative, *P. palmeri* S. Wats., restricted to the lower Sonoran Zone (Shreve and Wiggins, 1964). Because of its confusing characters and scarcity in collections, this taxon has been placed in various sections of *Prosopis* (Watson, 1889; Burkart, 1940; Schuster, 1969) or in a monotypic genus *Sopropis* (Britton and Rose, 1928). The most recent treatment of the Leguminosae by Hutchinson (1964) returned *P. palmeri* to a monotypic genus. We report here results of an overall study of *Prosopis* (Carman, 1973; Burkart, in press) that indicate *P. palmeri* should not only be retained in *Prosopis* but should also be placed in a section to which it has not previously been referred. In addition, our study of *P. palmeri* helps to confirm a decision to unite two former sections of the genus (Burkart, in press) and provides clues for the evolutionary history of *Prosopis*.

In a current revision of *Prosopis,* Burkart (in press) has separated the genus into five sections based on the morphological characters shown in Table 1. The largest section, *Algarobia,* contains the 29 species known as mesquites in North America and algarrobos in South America. The second largest section, *Strombocarpa,* formerly contained only the screwbeans (Burkart, 1940) but has been modified to include the two species

† Deceased

of the former section *Cavenicarpa*. Two screwbeans, *Prosopis pubescens* Benth. and *P. reptans* Benth., have traditionally been considered the only two native species of this section to occur in North America. The remaining species in sect. *Strombocarpa* (including *Cavenicarpa*) were previously thought to occur only in arid and semiarid areas of Central and southern South America. A third New World section containing only *P. argentina* Burk., a species restricted to the base of the Andes of northwestern Argentina, has only recently been circumscribed (Burkart, in press).

The remaining two sections of *Prosopis* are Old World. The four species of sect. *Prosopis* are scattered across Iran, Afghanistan, and India. *Prosopis africana* (Guill. & Perr.) Taub., the only member of sect. *Anonychium*, is common in the savannas of west-central Africa east to Ethiopia.

Many earlier treatments that dealt with *Prosopis* did not include *P. palmeri* because they restricted themselves to the species in the United States (Benson, 1941; Isely, 1972) or to only the taxa of sect. *Algarobia* (Johnston, 1962). The treatment of *Prosopis* by Shreve and Wiggins (1964) considered *P. palmeri* a *Prosopis* but did not indicate sectional affinities. In an earlier treatment, Burkart (1940) tentatively suggested a placement of *P. palmeri* near *P. africana*, and at least one subsequent author (Schuster, 1969) formally placed it with that species in sect. *Anonychium*. Finally, Hutchinson (1964) resegregated *P. palmeri* in the monotype *Sopropis* because its spines do not match those of species with similar fruits (sect. *Prosopis*) and the fruits do not match those of species with similar spine development (sect. *Strombocarpa*). In addition, Hutchinson (1964) decided that the partial fusion of the petals in *P. palmeri* was a unique character. It is noteworthy that he did not entertain the idea that *P. palmeri* might be allied to *P. africana*, a species with which he was very familiar.

Morphology

An examination of Table 1, which enumerates morphological characters of all of the currently recognized sections of *Prosopis*, clearly shows that the majority of features found in *P. palmeri* (fig. 1), including sympetally (fig. 1, d) are similar to those found in sect. *Strombocarpa*. Although absence of spines in *P. africana* does not, by itself, preclude a close relationship with *P. palmeri*, distinct differences in the internal fruit structure (fig. 1, e), *P. africana*'s dense rather than loose arrangement of flowers along the inflorescence (fig. 1, b), and the lack of conspicuous stipular spines that are present in *P. palmeri* (fig. 1, c) argue against any such alignment.

Palynology

A survey of the pollen of species of all sections of *Prosopis* using the scanning electron microscope reveals a uniformity of size and shape

TABLE 1. CHARACTERISTICS OF THE SECTIONS OF PROSOPIS COMPARED WITH P. PALMERI.

Section or taxon	Spines	Stipules	Inflorescence	Flower	Ovary
Prosopis	aculei along the branches	foliaceous	spicate, fls. loosely arranged	glabrous petals; white; free	glabrous
Anonychium	absent	inconspicuous	spicate, fls. loosely arranged	glabrous petals; white; free	villous
Algarobia	paired or single formed by lateral branches	inconspicuous	spicate, fls. densely or loosely arranged	pubescent petals; white, yellow or red; free	villous
Prosopis argentina Burk. (new section, Burkart, in press)	single, axillary and terminal	inconspicuous	spicate, fls. loosely arranged	pubescent petals; color uncertain; almost free	villous
Strombocarpa	paired, thin, white, or thick, yellow	forming the paired spines	spicate or globose; if spicate, fls. loosely arranged	pubescent or villous petals; yellow, reddish; fused	villous
Prosopis palmeri S. Wats.	paired, thin, white	forming the spines	spicate, fls. loosely arranged	glabrous petals; yellow; fused	villous

TABLE 1. *Continued.*

Section or taxon	Fruit shape	Mesocarp	Endocarp	Seeds	Chemistry
Prosopis	thick, slightly flattened, straight or arched	not developed	degenerates	end to end	M–3–0–g
Anonychium	thick, terete, straight	spongy	horizontally septate	end to end	no M–3–0–g
Algarobia	slightly flattened, straight or arched or twisted	spongy	stony, horizontally septate	end to end	M–3–0–g in only 2 of 29 species
Prosopis argentina Burk. (new section, Burkart, in press)	beaded, straight	reduced red	stony, horizontally septate	end to end	no M–3–0–g
Strombocarpa	spirally twisted or short, terete	disintegrates or dense, spongy	horizontally or transversally septate	end to end or stacked	M–3–0–g
Prosopis palmeri S. Wats.	slightly flattened, straight or slightly arched	disintegrates	disintegrates	end to end	M–3–0–g

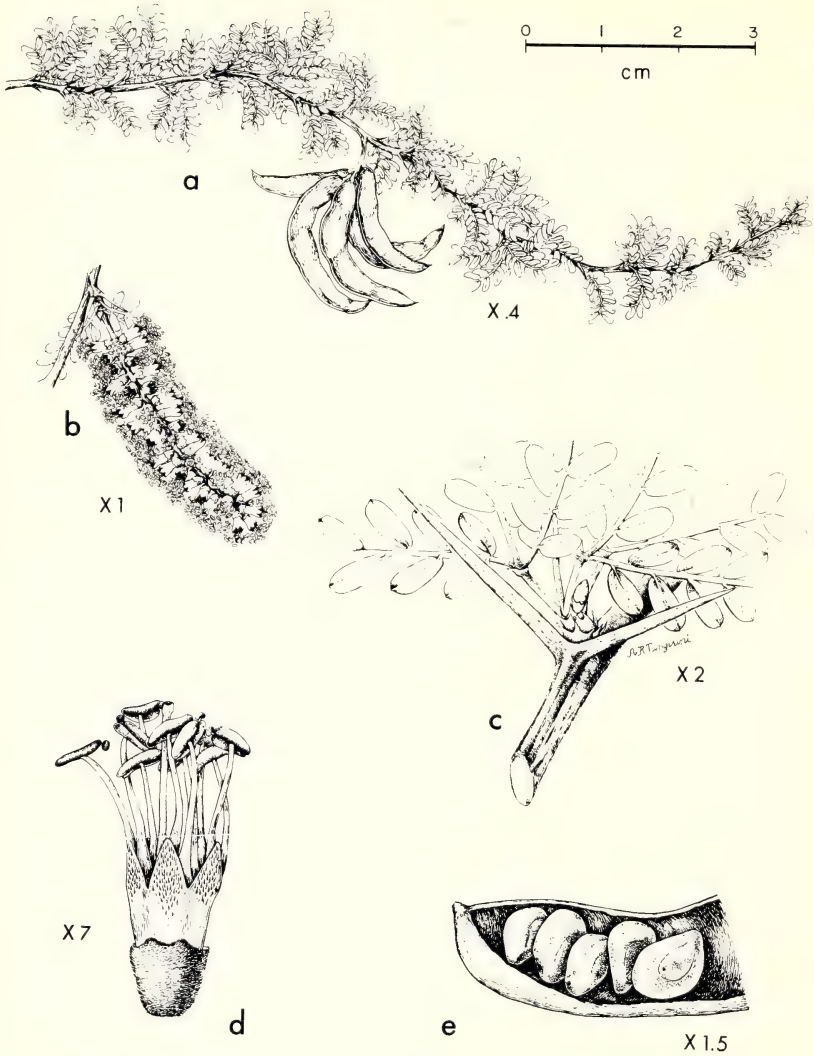

FIG. 1. Morphological features of *Prosopis palmeri* S. Wats. a, flowering branch of a tree 4m tall showing the clustering of the leaves on short shoots along the branch and the straight or slightly curved aspect of the pods. b, an inflorescence with the flowers rather loosely arranged along the spike. c, a pair of spines with axillary buds and shoots above demonstrating that the spines are formed from a pair of stipules. d, a flower illustrating the cuplike stigma and the anther glands found in all *Prosopis* species and the sympetalous corolla restricted to a few species. e, a cut-away section of a mature fruit that illustrates that the meso- and endo-carp have disintegrated. The seed on the far right has shaken loose and is upside down. The circular markings on the seeds are found throughout *Prosopis* and mark a weak region facilitating seed germination. Drawn from *Carter 2477* and *4275* (US) by Alice Tangerini.

throughout the genus. Slight variations that are present include a tendency for members of sect. *Algarobia* with single axillary spines to have more prolate pollen with smoother exines than grains of species of other groups. Pollen of sect. *Prosopis* is also very prolate but is punctate or rugose. Pollen of *P. palmeri* most closely resembles that of *P. pubescens* (sect. *Strombocarpa*) although both are similar to that of most species in the genus.

Natural Products Chemistry

As part of a study of the flavonoid chemistry of *Prosopis* (Carman, 1973), flavonoid compounds from the leaves of *Prosopis palmeri* were chromatographically and spectrally compared with those obtained from species in various sections. Results from the chemical analyses definitely indicate that *P. palmeri* belongs in *Prosopis*. The chemistry further supports exclusion of *P. palmeri* from sect. *Algarobia* or sect. *Anonychium*. Except for *P. alba* Griseb. and *P. chilensis* (Mol.) Stuntz (sect. *Algarobia*), the species of these two sections do not contain myricetin 3–0–glycosides, which are abundant in leaf extracts of *P. palmeri*. However, species of sects. *Adenopis* and *Strombocarpa* all produce a number of myricetin 3–0–glycosides (Table 1). Of the species in these two sections, only *P. pubescens* has a flavonoid pattern nearly identical to that of *P. palmeri* (fig. 2). Both have patterns relatively distinct from that of *P. reptans,* the second North American screwbean.

Conclusions

On the basis of similarities in floral morphology, pollen type, vegetative structure, and flavonoid chemistry (Table 1), *Prosopis palmeri* definitely belongs within *Prosopis* and should not be considered generically distinct. Presence of paired stipular spines (fig. 1, c) and of myricetin substituted glycosides indicates that it belongs in sect. *Strombocarpa*. The horizontal arrangement of the seeds (fig. 1, e) indicates its relationship within this section to the screwbeans. (These species are placed together in a series of sect. *Strombocarpa* and those species formerly placed in sect. *Cavenicarpa* in a second series, cf. Burkart, in press). The lack of coiling of the fruit is, however, novel in this group although *P. torquata* (Cav. ex Lag.) DC., a screwbean of northwestern Argentina and Chile, has fruits that only loosely spiral. In terms of flavonoid chemistry, pollen morphology, and leaf morphology, *P. palmeri* is most similar to *P. pubescens*. Nevertheless, the straight or arched fruit (fig. 1, a) with its disintegrating mesocarp and endocarp (fig. 1, e) is very different from that of the latter. The distinctness of the natural products chemistry between *P. pubescens* and *P. reptans* has already led to the postulation that these two North American representatives of sect. *Strombocarpa* represent two independent introductions from South America (Carman and Mabry, in press). The differences in the fruit

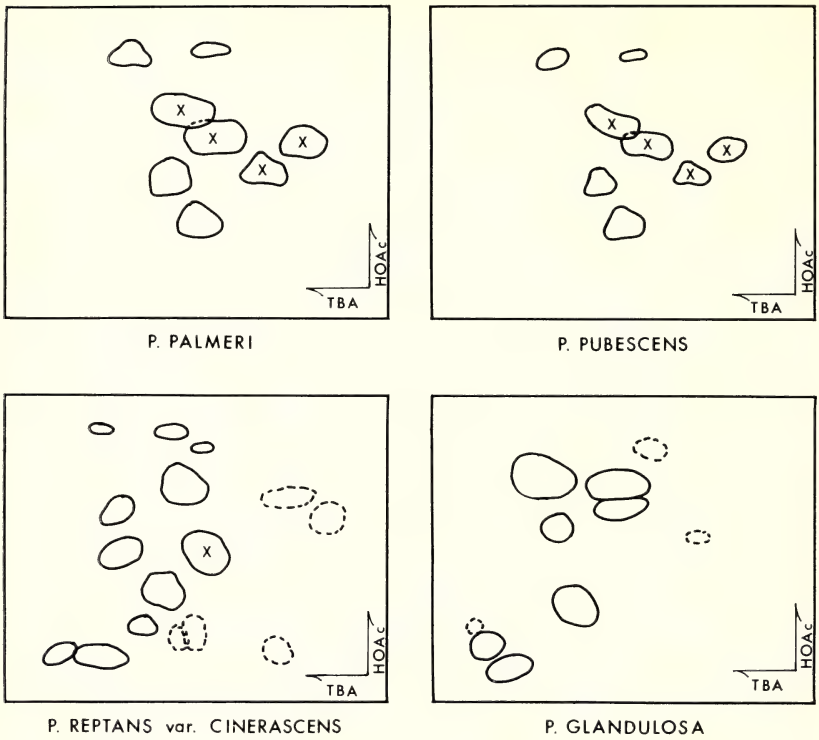

FIG. 2. Chromatograms showing flavonoid patterns of three members of sect. *Strombocarpa* (*Prosopis palmeri*; its nearest apparent relative, *P. pubescens*; and another North American species, *P. reptans* var. *cinerascens*) and also a member of section *Algarobia,* the common North American honey mesquite, *P. glandulosa.* Data from Carman, 1973, and *in litt.*

morphology between *P. palmeri* and either of these two species indicate a third and probably early independent colonization. The marked morphological differences between *P. palmeri* and the screwbeans and the presence of some similarities with Old World species imply that it reached North America early in the evolution of the genus and may have diverged little from the basal stock that subsequently gave rise to sect. *Strombocarpa.*

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DISTRIBUTION, CHROMOSOMES, AND TAXONOMY OF PARTHENICE MOLLIS (COMPOSITAE)

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Parthenice is a little-known genus native to southern Arizona and northwestern Mexico. Its single species, *P. mollis* A. Gray, is a rank-smelling, weedy annual bearing a superficial resemblance to *Iva xanthifolia* (marsh elder).

In 1851, Charles Wright made the first known botanical collection of *P. mollis* near the Mexican town of Santa Cruz, Sonora. Since that time the plant has been rather sporadically collected in Arizona as well as in several states in Mexico (fig. 1). In addition, *P. mollis* has been reported from New Mexico and Colorado in several western United States floras. Weber (1966) stated, however, that he was unable to verify the report of *P. mollis* in Colorado and suggested that the record should be rejected. The report from New Mexico also seems doubtful; there are no supporting records in herbaria of that state. It is interesting to note that the type specimen bears the handwritten inscription "collected in N. Mex.", which may have been interpreted to mean New Mexico instead of northern Mexico thereby giving rise to the report from that state.

In Arizona, the Ajo Mountains represent the western limit of distribution; the Patagonia Mountains limit it to the east and the Tortolito Mountains are the most northern site. The rather colonial populations

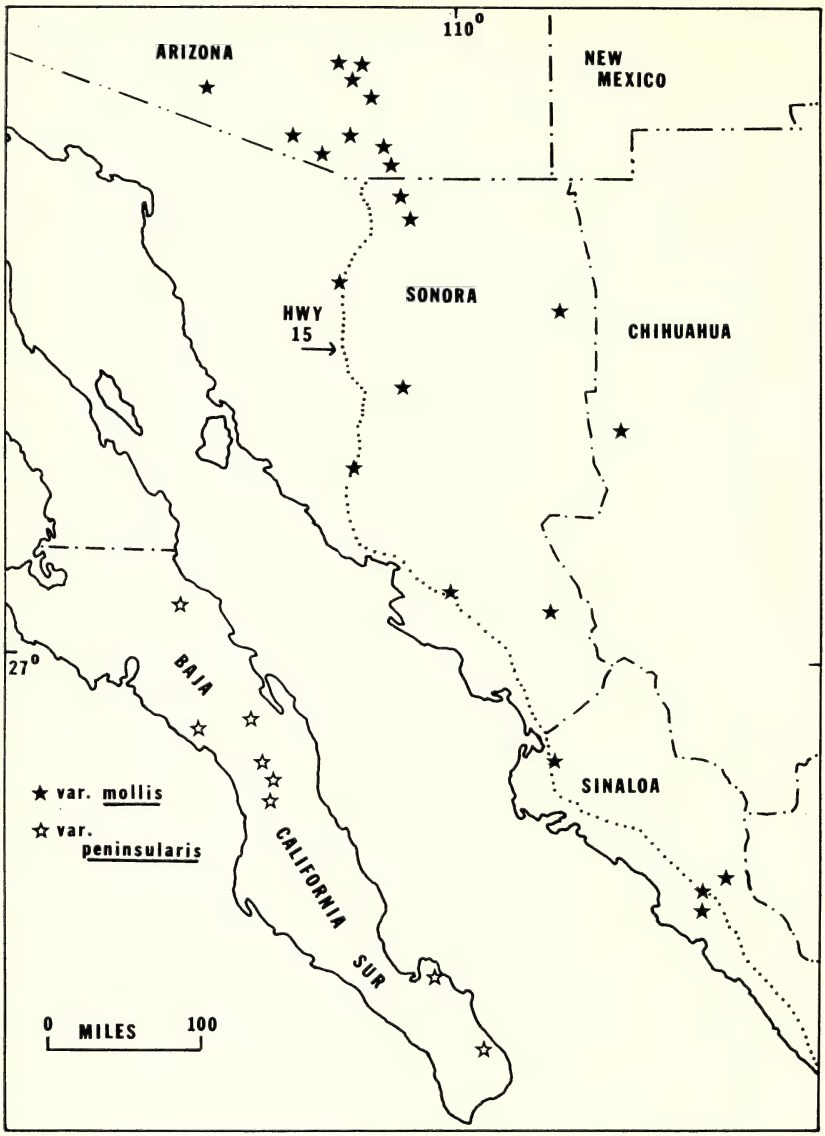

FIG. 1. Documented distribution of *P. mollis* var. *mollis* and *P. mollis* var. *peninsularis* in the southwestern United States and northwestern Mexico.

are most frequently found along washes or roadside embankments having a distinct southern exposure. In Mexico, I found it to be a conspicuous roadside weed from Nogales, Sonora, to Culiacan, Sinaloa. North of Hermosillo the species can be found on hillsides and in washes associated with west and north flowing river basins of the Rio Magdalena and the

Santa Cruz. South of Hermosillo it appears to be restricted to roadcuts and *milpas* mainly near Highway 15. In Baja California Sur, *P. mollis* has been collected in dry lake beds or *playas* and arroyos.

Parthenice is essentially a plant of the Sonoran Desert in sense of Shreve and Wiggins (1964). Frequently found in the Upper Sonoran Life Zone at 950 to 1400 m (3,000 to 4,500 ft), it also occurs at sea level near Guaymas, Sonora. Few data are available for elevations of *Parthenice* in Baja California Sur; one collection (*Carter 5050*) indicates an elevation of 360 m (1,200 ft) near San Javier.

Chromosomes

Good meiotic figures were obtained from aceto-carmine squashes of pollen mother cells from young florets whose stamens possessed no yellowish color. A modified Carnoy's solution (chloroform:ethanol:acetic acid, 4:3:1, v/v) was used for killing and fixing. Collections made between 8:30 and 9:30 a.m. gave the greatest number of dividing cells, although figures could be obtained at any time of day. Counts from plants grown in the greenhouse at the University of Arizona indicated $2n = 18$ II for *P. mollis* var. *mollis* near Tucson, Arizona. Dr. T. F. Stuessy and Dr. D. J. Keil have the same count from two Mexican populations (pers. comm., 1975). Chromosome vouchers (marked *) are cited with representative specimens. [Note added in proof: Urbatsch (Southw. Naturalist 20:283–285. 1975) reported $2n = 18$ II for *P. mollis* (Baja California, ca 1 mi NE of San José de Commandú, *Urbatsch 1202,* TEX).]

Taxonomy

Gray (1853) considered *Parthenice* closely related to *Parthenium* (guayule) in the Melampodiinae (Heliantheae). He distinguished *Parthenice* from *Parthenium* by the former's deciduous and less ligulate ray corollas, reduction of the paleae of the disk to minute rudiments, and lack of a pappus.

Since 1853 little has been done to alter the taxonomic position of *Parthenice*. Baillon (1882) gave *Parthenice* and *Aiolotheca,* a name of a scarcely known genus from San Luis Potosí, as synonyms of *Parthenium* yet recognized them as sections of that genus. No new nomenclatural combinations were made nor was any justification given for such a treatment. Rollins (1950) pointed out that the differences between these genera are so apparent that no modern taxonomist would consider them congeneric. Rzedowski (1968) reviewed material identified as *Aiolotheca* and found it to be *Zaluzania* (Verbesininae).

Although *Parthenice* has been traditionally placed in the Melampodiinae, a taxon that Gray (1884) and others (see Stuessy 1973 for a review) regard as artificial, its true affinity has not yet been established. Bentham (1873) suggested the intermediate nature of the genus in his frequently quoted passage wherein he relates the Anthemideae with the Melampodiinae through *Parthenice*.

Work by palynologists has led to other speculations. Wodehouse (1935) relates *Parthenice* to Ambrosiinae (Heliantheae) because its pollen possesses a combination of characters that make it appear to be an ideal prototype for that subtribe. Pollen studies with the electron microscope (Skvarla and Larson, 1965; Skvarla and Turner, 1966) substantiate the work of Wodehouse only in part. Pollen of *Parthenice* appears to be the prototype for only certain members of the Ambrosiinae. Skvarla and Turner (1966) conclude ". . . *Parthenice* is not an easy genus to place and it might be that the genus, phyletically speaking, stands somewhere within the aggregate triangle Heliantheae-Ambrosieae-Anthemideae".

In apparent contradiction to palynological data, anatomical data derived from study of embryo sac development and stem anatomy substantiate the relationship between *Parthenium* and *Parthenice* (Sauck, 1969). Therefore, a true picture of the position of these genera may not be obtained without an examination of data from many sources.

Parthenice mollis is treated here as being composed of two varieties that may be readily distinguished by the length of the pales that are attached to the achene (fig. 2). In material from Arizona, Sonora, Sinaloa, and Chihuahua, the pales are longer than the body of the achene, while plants having achenes with pales shorter than the body of the fruit are confined to Baja California Sur. This treatment was suggested to me several years ago by Miss Annetta Carter who also proposed the name "peninsularis" for the plants from Baja California Sur.

PARTHENICE MOLLIS A. Gray, Smithsonian Contr. Knowl. 5(6):85–86. 1853. TYPE: Mexico, Sonora, Santa Cruz, mountain ravine, Sep 1851, *Charles Wright 1208*. (Holotype: GH)

Plants aromatic, cinereous-puberulent erect annuals to 2 m. Stems normally unbranched except in the inflorescence. Leaves various, alternate; those below the inflorescence triplinerved, ovate to deltoid, long petioled, some with lamina decurrent on the petiole for several centimeters, toothed to coarsely crenate, lower leaves becoming quite large, up to 30 cm long; leaves of the inflorescence smaller, 1–7 cm long, ovate-lanceolate, toothed to entire. Cotyledons small, 1 mm in diameter, simple, glabrous, ovoid, petioled at maturity. Capitula hemispherical, numerous, panicled, sessile or pedunculate, greenish-white, densely glandular. Phyllaries in two distinct series, the outer series 5, ovate, herbaceous, overlapping, somewhat reflexed with age, the inner series 8, hyaline, broadly ovate to nearly round, distinctly cupped to fit the achene but not fused to it, deciduous. Receptacle convex, paleaceous with two types of pales; those associated with the ray flowers coriaceous, linear, purple mottled, curved at the apex, deciduous and attached to the achene at maturity; those associated with the disk flowers minute, conical, hollow, persistent. Ray flowers 8, pistillate, corollas minute, greenish, densely glandular, scarcely ligulate, stigma branched, papillate. Disk flowers staminate,

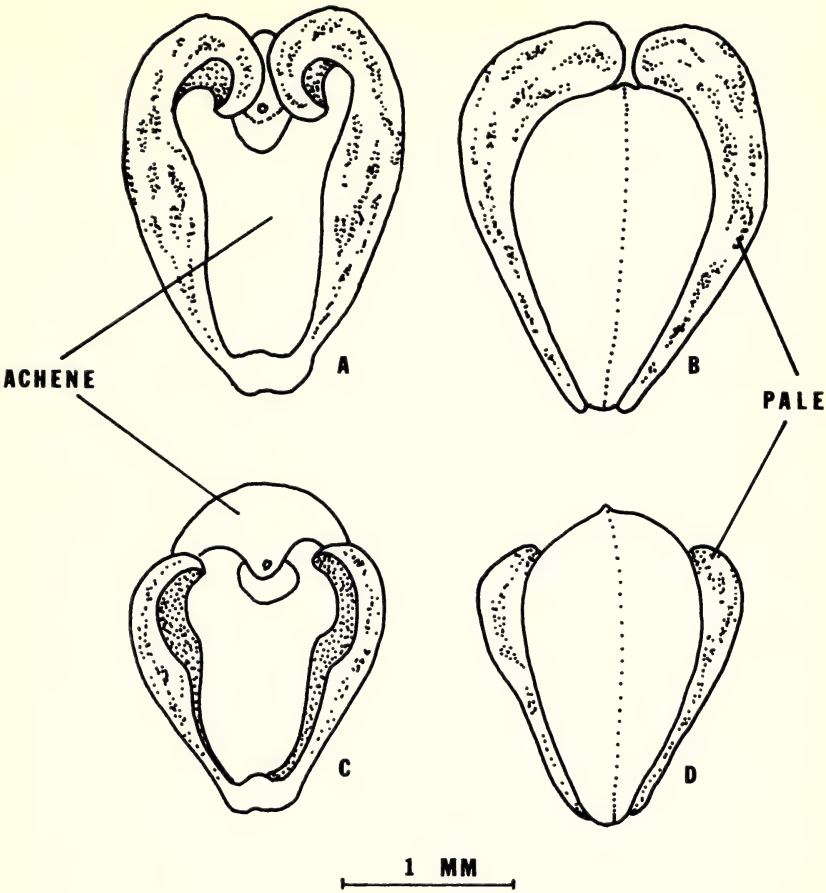

FIG. 2. Comparison of achenes of *P. mollis* varieties. A, ventral view, and B, dorsal view, var. *mollis;* C, ventral view, and D, dorsal view, var. *peninsularis.*

the pistil rudimentary, the corolla five-toothed, actinomorphic, densely pubescent and glandular at the apex, greenish-yellow, stamens 5, loosely coherent, tipped with a deltodid appendage, stigma of the brush type, unlobed, flower shortly pedicellate, the pedicels remaining attached to the receptacle after the dehiscence of the flower. Pollen tricolpate, echinate, yellowish, oblong when dry, columellae branched, foramina absent. Achenes dorsoventrally flattened, obovate, tuberculate, glabrous, sessile, apiculate, falling away at maturity with the pales of the opposed disk flowers. Pappus none on the disk flowers, occasionally represented by a tooth in the ray flower. Hairs of two types; a uniseriate clothing hair and a biseriate glandular hair. Chromosome number $2n = 18$ II.

1. PARTHENICE MOLLIS var. MOLLIS.

Wings of the achene longer than the body of the fruit.

Distribution (fig. 1): Mexico: Sonora, Sinaloa, Chihuahua; United States: southern Arizona (Pima, Santa Cruz, Cochise counties); frequently along washes or amongst boulders having a distinct southern exposure. In Mexico, often along roadsides in disturbed sites where runoff moisture is available. Jul-Aug.

Representative specimens: United States: Arizona: Cochise Co.: 2.5 mi SW of Willcox, Sep 1970, *Page s.n.* (ARIZ); Pima Co.: S end of Coyote Mts., 18 Nov 1960, *Barr and Goodding 60–385C* (ARIZ); along Alamo Wash, Organ Pipe National Monument, 12 Sep 1943, *Clark 11015* (GH); Toro Canyon, Baboquivari Mts., 29 Aug 1931, *Gilman 55* (ARIZ); Baboquivari Mts., 27 Dec 1935, *Goodding 9140?* (ARIZ); W side Mt. Baboquivari, 6 Oct 1944, *Gould, Darrow, and Haskell 2683* (ARIZ, CAS, UC); lower part of Baboquivari Canyon, 15 Aug 1926, *Peebles, Harrison, and Kearney 2790* (ARIZ); Box Canyon, Santa Rita Mts., 27 Aug 1964, *Reese 1* (ARIZ, CAS, ASU); Sabino Canyon, Santa Catalina Mts., 29 Aug 1964, *Reese 2* (ARIZ, CAS, ASU); Redington Pass Road, southern tip of the Santa Catalina Mts., 2 Sep 1964, *Reese 3* (ARIZ, ASU, CAS, UC); Brawley Wash, Baboquivari Mts., 19 Sep 1964, *Reese 6* (ARIZ); one mi S of Tubac, 2 Oct 1964, *Reese 7* (ARIZ, ASU, CAS, UC); Wild Burro Canyon, Tortolito Mts., 25 Oct 1964, *Reese 12* (ARIZ, ASU, CAS, UC; *greenhouse—Univ. Arizona, from seed from Redington Pass, 17 Jul 1966, *Reese 168* (ARIZ, UC, CAS); near Pacing Horse Ranch, Canyon del Oro, Santa Catalina Mts., 9 Aug 1966, *Reese 171* (ARIZ, ASU, CAS, UC); Pontatoc Wash, foothills Santa Catalina Mts., 7 Aug 1968, *Reese 208* (ARIZ, ASU, CAS); Canyon del Oro, corner of Tangerine Road and the Oracle Hwy, 25 Aug 1968, *Reese 212* (ARIZ, ASU); seedlings, near Canyon del Oro, Pacing Horse Ranch, 7 Feb 1969, *Reese 213* (ARIZ, ASU); Fort Lowell, 10 Sep 1903, *Thornber s.n.* (ARIZ); Stone Cabin Canyon, Santa Rita Mts., 12 Sep 1903, *Thornber 130* (ARIZ, CAS, DS, UC); Santa Cruz Co.: road to Lochiel, Patagonia Mts., 2 Oct 1964, *Reese 8* (ARIZ, ASU, CAS, UC); Sycamore Canyon, near Ruby, 30 Sep 1944, *Darrow and Haskell 2079* (ARIZ, UC); Patagonia Mts., 24 Aug 1940, *Kearney and Peebles 14821* (ARIZ); Sycamore Canyon, 18 Aug 1968, *Reese 209* (ARIZ, ASU); on dam of Peña Blanca Lake, 18 Aug 1968, *Reese 211* (ARIZ, ASU).

Mexico: Chihuahua: Rio Aros, 23 July 1937, *LeSueur s.n.* (GH, UC); Sinaloa: on hillside roadcut 14 mi N of Culiacan, 29 Aug 1966, *Reese 182* (ARIZ, ASU, CAS, UC); Maraton, 12 mi W of Culiacan, Aug 1944, *Gentry 7059* (GH); Palmar, 50–70 mi N of Guamuchil, 22 Aug 1941, *Gentry 6102* (ARIZ, DS); Ymala (Imala), 16–25 Aug 1891, *Palmer 1430* (ARIZ, DS, UC, GH); *1.3 mi E of Cofradía, 25 Aug 1973, *Stuessy and Gardner 3038* (OS); Sonora: 31 mi S of border on Hwy 15, 23 Aug 1966, *Reese 172* (ARIZ, ASU, CAS, UC); first wash S of police station, Santa Ana, 23 Aug 1966, *Reese 173* (ARIZ, ASU, UC); 10 mi S of Benjamin Hill, along Hwy 15, 23 Aug 1966, *Reese 174*

(ARIZ, ASU, CAS, UC); 5 mi S of Oasis, 23 Aug 1966, *Reese 175* (ARIZ, ASU, CAS, UC); along road to Ures, 24 Aug 1966, *Reese 176* (ARIZ, ASU, CAS, UC); 36 mi W of Cananea, 24 Sep 1966, *Reese 183* (ARIZ, ASU, CAS, UC); 30 mi S of Hermosillo, 24 Aug 1966, *Reese 177* (ARIZ, ASU, CAS, UC); along Hwy 15, 60 mi S of Guaymas, 26 Aug 1966, *Reese 179* (ARIZ, ASU, CAS, UC); S of Santa Cruz, 2 Oct 1964, *Reese 11* (ARIZ, CAS, UC); La Matancita, 1 mi W of El Tigre, 30 Aug 1941, *White 4164* (ARIZ); Horconcitos, Arroyo del Salto, 6 Sep 1940, *White 3786* (GH); Rio Bavispe, 30 Aug 1941, *White 4164* (ARIZ, GH, UC); 12 mi S of Imuris, 24 Sep 1966, *Reese 184* (ARIZ, CAS, UC); Puerto de Huepari, NW of Aribabi, Rio Bavispe, 7 Sep 1939, *White 2771* (GH); San Bernardo, Rio Mayo, 24 Aug 1935, *Gentry 1622* (ARIZ, GH, UC); Santa Cruz, 1834, *Thornber 947* (UC); along stream where road from Alamos to San Pedro crossed the stream, 30 Jul 1969, *Mason 2916* (ARIZ, CAS, UC); *8.4 mi S jct rte 15 and road to Querobabi, 22 Aug 1973, *Stuessy and Gardner 3007* (OS).

2. **Parthenice mollis** var. **peninsularis** Sauck, var. nov. Type: Mexico, Baja California Sur, "La Laguna", hills east of La Paz; margin of a large rain basin, *Parkinsonia* association, 31 Mar 1949, *Annetta Carter 2615* (Holotype:UC; Isotype:GH).

Differt a var. *mollis* alis achenii fructificatione brevioribus. Plantae limitae ad Californiam Inferiorem.

Differs from var. *mollis* in that the wings of the achene are shorter than the body of the fruit.

Distribution (fig. 1): Moist arroyo margins, hillsides and slopes, dry lake bottoms; Baja California Sur: Tres Vírgenes north of Santa Rosalía, south to La Paz and Santiago in the "Cape" region. Feb–Apr.

Representative specimens: Mexico: Baja California Sur: SW side of Tres Vírgenes, 6 Mar 1935, *Wiggins 9727* (DS, UC); San Gregorio, 1 Feb 1889, *Brandegee s.n.* (UC); 13 mi W of Canipole, 16 Mar 1935, *Shreve 7112* (DS, ARIZ); Las Cuevitas, below Comondú, 17 Feb 1939, *Gentry 4233* (DS, UC); camp and hillsides near Comondú, 26 Apr 1931, *Wiggins 5491* (CAS, DS, GH, UC); side arroyo heading into Mesa San Alejo, SW of Rancho El Horno, 13 Mar 1960, *Carter and Ferris 3767* (UC); broad arroyo N of San Javier, 29 Sep 1965, *Carter 5050* (UC); Los Dolores, Apr 1892, *Bryant s.n.* (UC); Arroyo Quisapol, E of La Presa along trail to Laguna Caquihui, Sierra de la Giganta, 18 Nov 1959, *Wiggins 15560-A* (DS); La Paz, 20 Jan–Feb 1890, *Palmer 66* (GH); La Paz, 2 Feb 1890, *Brandegee s.n.* (UC); Santiago, *Jones 24626* (UC).

Acknowledgments

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Martin, University of New Mexico, and Dr. D. Gordon, New Mexico State University, for their time in attempting to verify the report of *P. mollis* in New Mexico. A summer research grant made possible through the efforts of the late Coordinator of Research at the University of Arizona, Dr. David L. Patrick, is gratefully acknowledged. This paper is a part of a Doctoral Dissertation completed at the University of Arizona in June, 1969.

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Occurrence of Oaks in Late Pleistocene Vegetation in the Mojave Desert of Nevada.—The nature of Pleistocene environmental change in Southwestern deserts is not well known. Quaternary fossil plant remains comparable to those found in eastern North America were thought to be non-existent in these deserts until Wells and Jorgensen (Science 143:1171–1174. 1964) reported that ancient wood rat middens are sources of abundant plant material. Modern wood rats(*Neotoma* spp.) gather most of the plant material found in their middens within thirty meters of the site (R. B. Findley, Univ. Kans. Publ. Museum Nat. Hist. 10:514–523.. 1958.), and fossil middens presumably also represent strictly local vegetation. Studies of such remains, together with advances in palynology, are providing evidence that changing vegetation has greatly altered the desert landscape during the last 40,000 years.

Two species of oaks, *Quercus chrysolepis* and *Q. dunnii,* not previously reported in late Pleistocene vegetation of the Mojave Desert, were found by the author to be present in ancient wood rat middens located in the Newberry Mountains, south of

Las Vegas, Nevada. It is unlikely that the vegetation of the area has been much altered by either ancient or recent human activities, particularly because the plant cover is too sparse to carry fire. Creosote bush *(Larrea tridentata)* is dominant up to about 1,100 meters on the alluvial fans that cover most of the area. Pinyon *(Pinus monophylla)*, oak *(Quercus turbinella)*, and juniper *(Juniperus californica)* are generally dominant above that level, although juniper also extends to a slightly lower level (above 950 meters). *Quercus turbinella* and *Juniperus californica* extend to less than 800 meters on several mesic sites. On the summit of Spirit Mountain, at about 1,700 meters, there is a small previously unreported population of *Quercus chrysolepis.*

Thirty wood rat midden sites were found in the study area (about 0.8 km^2) of granitic outcrops at about 850 meters elevation. The middens consisted of compact, indurated plant matter and dung, blackened and cemented with dried urine. They are found in crevices, under overhangs, and in shallow caves. Of the thirty sites inspected for woody plant remains, two contained pinyon, oak, and juniper; two had juniper and oak; one had oak only; nineteen had juniper only; and the contents of six are undetermined. Remnants of acacia, purshia, yucca, and some unidentified seeds and fragments were also recovered. Scrub oak *(Q. turbinella)* and juniper *(J. californica)* grow in the midden area at present, far below their normal altitudinal limit, growing in protected pockets that receive runoff from large rock exposures.

Radiocarbon dating was carried out with materials from a site selected because it contained the largest quantity and best preserved remnants of woody plants no longer growing in the immediate vicinity. There was a lens of *Pinus monophylla* needles in the midden material that was dated at 13,380 ± 300 years B.P. (Gak-1988). At this site another stratum of midden material contained remnants of *Quercus dunnii* (*Quercus palmeri* Engelm.) and perhaps *Quercus chrysolepis,* although remnants of the latter are too poorly preserved to be positively identified. Acorns from this stratum were dated at 9,500 ± 240 years B.P. (A–1017).

P. J. Mehringer studied middens from Sacatone Wash, 3.6 km south of this site, at 730 meters. These also yielded *Pinus monophylla* and *Quercus dunnii* and have been dated, respectively, at 19,620 ± 600 years B.P. (I–3659) and 9,490 ± 150 years B.P. (I–3669) (Mehringer, pers. comm.). Although Quaternary oak remnants in fossil wood rat sites are abundant in the Chihuahuan Desert (P. V. Wells, Science 153:970–974. 1966), this area is the first reported location for fossil late Pleistocene oak from the Mojave Desert.

Local evidence indicates an altitudinal depression for pinyon of over 300 meters during the late glacial. This agrees with evidence from elsewhere in the Mojave that the lower limit of the pinyon-juniper woodland lay at least 60 meters below its present level (P. V. Wells and R. Berger, Science 155:1640–1647. 1967). The local intrusion of *Quercus dunnii,* and perhaps also of *Quercus chrysolepis,* in early post-pluvial time is indicative of climatic warming. *Quercus dunnii* no longer occurs in the region at all, although Spirit Mountain offers some habitats that seem suitable for it. Although an altitudinal depression of 800 meters is suggested for *Quercus chrysolepis* since 9,500 B.P., this displacement might not be due solely to the regional temperature shift. The midden area rock rapidly channels runoff into pockets of soil at the base of the cliffs. These outcrops provide shade that permits the growth of *Quercus turbinella* far below its present average lower limit. *Quercus chrysolepis* could have occupied this habitat in a similar manner. The elevational change of pinyon that occurs under open slope conditions may not be directly comparable to the elevational change of *Quercus chrysolepis,* which today occupies more mesic microhabitats.

I am grateful to John Tucker, Department of Botany, University of California at Davis, for identification of modern fossil oaks; to Austin Long and Paul S. Martin, Department of Geosciences, University of Arizona, for radiocarbon dates; and to Peter Mehringer, Department of Anthropology, University of Utah, for generously sharing information on fossil wood rat nests.—Paul H. Leskinen, Department of Geography, Bowling Green State University, Bowling Green, Ohio 43403.

Seed Longevity of the Sierra Gooseberry.—*Ribes roezlii* Regel, the Sierra Gooseberry, is the most abundant species of *Ribes* L. in the main timber belt on the western slope of the Sierra Nevada. This ribes attains greatest abundance and vigor on severely disturbed sites on relatively deep and well-developed soils. Barring immediate development of dense brush after forest disturbance, such sites also are the most productive for growing timber. The characteristically prompt occurrence of moderate to vast numbers of gooseberry seedlings on these sites was most readily explainable—even forty years ago—by the "storage" of innumerable viable seeds in the forest floor.

In the fall of 1931, Frank A. Patty, a forest ecologist, collected a supply of ripe gooseberry fruits from numerous bushes on a recently logged area in the vicinity of Pinecrest, Tuolumne County, California. A handful of fruits was mixed with fine river sand from a bar on the South Fork Stanislaus and placed in the bottom of each of about two dozen quart milk bottles. The bottles were buried "bottoms-up" at the bottom of a trench dug about 50 cm deep in the forest floor under a medium-density forest canopy on a gentle slope.

Two bottles were dug up on 15 Sep 1971, 40 years after they had been buried, and transferred to a household refrigerator.

Contents of the bottles were slightly moist when dug. The layer of sand and seeds at the bottom of the bottles contained considerable disintegrated organic matter. The seeds were very dark, almost black, and hardly distinguishable as seeds—and fewer per bottle than expected. Presumably some of the seeds, along with the fruit pulp and skins, had rotted. A few small live conifer roots were found in the neck of one bottle.

Seeds in one sample bottle were separated from the sand on 23 Sep 1971 by drying on paper in a cool basement and by sieving and winnowing. The second sample remained in the refrigerator until 4 Dec 1971, and the seeds were then separated as before. Three germination tests each of 100 cleaned seeds were started on 23 Sep and four more on 4–7 Dec 1971. Culture containers were small shallow "tuna cans", #2½-size cans (about 10 cm across and 11.5 cm deep), or tarred-paper plant bands (about 7.6 cm square and 7.6 cm deep). Washed river sand was "pasteurized" by heating wet sand over boiling water in a large, covered double-boiler for about three hours. The heat-treated sand was then cooled, put into the culture containers, and compacted. Seeds were counted and planted 6 to 9 mm deep. Ferbam (ferric dimethyldithiocarbamate), a fungicide that seems to do no harm to seeds, was distributed over the surface of the cultures and watered-in. Cultures were periodically inspected, remoistened, and re-treated with ferbam as deemed advisable.

All cultures were kept under good germinative conditions for a year or more, and all went through at least two complete cycles of stratification-germination temperatures. Cultures in small cans commonly were stratified in a household refrigerator and germinated in a basement. Cultures in the larger containers, whenever possible, were stratified by keeping them outside against a north wall during cool to cold weather and were germinated in warm weather under the half-shade of lath covers.

The seven cultures produced a few more than 50 seedlings. Cultures started in September, in general, produced more seedlings than those started in December. Tests in larger containers produced many more seedlings per culture than tests in smaller containers. Also, in the larger containers many more seedlings resulted from a second stratification-germination cycle rather than from the first. Average seedling production per culture of 100 seeds was 1.3 in the first cycle and 6.0 seedlings in the second cycle, an overall mean of 7.3 seedlings.

Obviously some Sierra gooseberry seeds remain viable after storage in the soil of the forest floor for 40 years.

The exact number of bottles remaining in the buried seed cache is unknown, but there are presumed to be six at least. Plans are to recover one or two bottles at 5-year intervals. Thus a set of germination tests on recently exhumed seed is planned for the fall of 1976.—C. R. Quick, Route 1, Box 318, Clarksburg, California 95612, and F. A. Patty, 774 Spruce St., Berkeley, California 94707.

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RE-EVALUATION OF CUPRESSACEAE AND TAXODIACEAE: A PROPOSED MERGER

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Among the many interesting coniferous trees, those referred to Taxodiaceae and Cupressaceae are particularly noteworthy to both botanists and laymen. Foremost among these are such restricted endemics as the taxodiaceous coast redwood (*Sequoia sempervirens*) and bigtree (*Sequoiadendron giganteum*), but species of the cupressaceous genera *Cupressus, Juniperus, Thuja, Chamaecyparis,* and *Calocedrus* have also been frequently discussed. Familial classification of these and other conifers has seemed an unlikely source of controversy since Pilger (1926) decisively split the classical Pinaceae (Abietineae) into seven families: Taxaceae, Podocarpaceae, Araucariaceae, Cephalotaxaceae, Pinaceae s. s., Taxodiaceae, and Cupressaceae. Florin (1948) discussed the reproductive morphology of the taxads and concluded that they should be segregated from Pilger's other families in a separate order Taxales. In line with his suggestion they are omitted from discussion here. Pilger's delimitations of the other families have remained virtually unchallenged by taxonomists, who have concentrated instead on many perplexing problems at other taxonomic levels (Florin, 1955; Janchen, 1950). The six-family scheme has also served as the framework for presentation of results of virtually all modern reviews of such aspects of conifers as epidermal characters (Florin, 1931), external leaf morphology (de Laubenfels, 1953), wood anatomy (Greguss, 1955; 1972), shoot apex (Johnson, 1951), chromosome number (Khoshoo, 1961), male gametophyte (Sterling, 1963), female gametophyte (Maheshwari and Singh, 1967), embryogeny (Doyle, 1963; Doyle and Brennan, 1971; 1972; Roy Chowdhury, 1962), pollination (Doyle, 1945b), structure of megasporangiate strobilus (Florin, 1951), phytochemistry (Hegnauer, 1962), and geographical distribution (Buchhold, 1948; Florin, 1963; Li, 1953b).

Circumscriptions of the families segregated by Pilger and accepted by subsequent authors are based on a number of vegetative and reproductive characters, but primary distinctions are derived from the structure of their megasporangiate strobili (Pilger, 1926; Sporne, 1965). All are separable on this basis except Cupressaceae and Taxodiaceae, which show fundamental similarities in development and final form of the ovuliferous scale-bract complexes (Florin, 1951). These two families, in contrast to all other pairs of conifer families, are usually distinguished only by leaf form and phyllotaxis. Most modern authors have

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recognized a close relationship between these two families but have kept them separate (Takhtajan, 1953).

I have come to believe that the genera usually assigned to Cupressaceae and Taxodiaceae should be assigned to one family, which must, for reasons of priority, be called Cupressaceae. Two lines of evidence are fundamental to this proposition. Both groups of genera taken together show the same degree of morphological cohesiveness as other single conifer families. As a group they share a distinctive array of vegetative and reproductive characters that separate them from the equally distinctive Podocarpaceae, Araucariaceae, Cephalotaxaceae, and Pinaceae. Furthermore, *Sequoia* and its allies are as closely related to *Cupressus* (which is similar to the probable ancestor of many northern hemisphere cupressaceous genera) as they are to other genera usually included with them in a segregate family. They are likewise related to *Callitris* and other southern hemisphere cupressaceous genera. The latter are less closely allied to *Cupressus* than are their northern hemisphere counterparts and probably represent two or three lineages coordinate with the *Cupressus*-line and linked to it by a common taxodiaceous ancestor.

The group of twenty-eight genera in question has a wide geographical distribution in temperate regions (Table 1), comparable to those of the other large conifer families, Pinaceae and Podocarpaceae, though more bihemispheric than either of these (Florin, 1963). While most modern systematists have accepted segregation of these genera into two families, agreement on this arrangement is relatively recent and older treatments often group them along rather different lines. Linnaeus (1753) described *Taxodium distichum,* the only taxodiaceous tree known to him, as a species of *Cupressus,* just as Poiret (1817) subsequently first described *Glyptostrobus lineatus* as a species of *Thuja.* Similarities among some genera are also reflected in such specific epithets as "cupressoides" (*Athrotaxis, Fitzroya, Widdringtonia*), "glyptostroboides" (*Metasequoia*), "cryptomerioides" (*Taiwania*), and "thyoides" (*Chamaecyparis*).

Families recognized by early students of the Coniferales often had quite different circumscriptions than those accepted by Pilger (1926). Endlicher (1847) placed all conifers in four families (for convenience I use the term family for the taxonomic grouping generally called order or *ordo naturalis* by nineteenth century botanists) and included in two of them all genera here referred to Cupressaceae s. l. Endlicher's Cupressineae comprised all cupressaceous genera as well as *Taxodium, Glyptostrobus,* and *Cryptomeria,* while other taxodiaceous genera were included with *Agathis* (Araucariaceae) in a tribe of his Abietineae. Gordon (1880), in contrast, recognized only two families of conifers. Cupressaceous and taxodiaceous genera are found in all three tribes of his Pinaceae. Most of these genera constituted his tribe Cupresseae, while *Juniperus* was placed in a monotypic tribe and *Cunninghamia, Athrotaxis,* and *Sciadopitys* together formed a "section" included in his

tribe Abietineae along with "sections" for the araucarians and abietineans. Other variations are displayed in important taxonomic systems of Gordon (1858), Carrière (1867), Parlatore (1868), Masters (1893), and Vierhapper (1910). Most commonly in these and other systems the

TABLE 1. NEW ARRANGEMENT OF CUPRESSACEAE BARTLING, 1830 (INCL. TAXODIACEAE WARMING, 1884). Column a: genera formerly assigned to Taxodiaceae (T) or to Cupressaceae (C). Column b: number of species. Column c: generalized distribution.

	a	b	c
Subfamily Sciadopitoideae Saxton, 1913			
Sciadopitys Siebold & Zuccarini, 1842	T	1	Japan
Subfamily Cupressoideae K. Koch, 1873			
Tribe Cupresseae Dumortier, 1827			
Subtribe 1			
Sequoia Endlicher, 1847	T	1	Calif.
Sequoiadendron Buchholz, 1939	T	1	Calif.
Subtribe 2			
Metasequoia Hu & Cheng, 1948	T	1	China
Subtribe 3			
Cupressus Linnaeus, 1753	C	ca 15	N.Hemis.
Chamaecyparis Spach, 1842	C	6	N.Hemis.
Fokienia A. Henry & Thomas, 1911	C	2	China
Platycladus Spach, 1842 (=*Biota* Endlicher, 1847)	C	1	China
Thujopsis Siebold & Zuccarini, 1842	C	1	Japan
Thuja Linnaeus, 1753	C	5	N.Hemis.
Microbiota Komarov, 1923	C	1	Siberia
Calocedrus Kurz, 1873 (= *Heyderia* K. Koch, 1873)	C	3	N.Pac.
Juniperus Linnaeus, 1753 (incl. *Arceuthos* Antoine & Kotschy, 1854)	C	ca 60	N.Hemis.
Subtribe 4			
Callitris Ventenat, 1808 (incl. *Octoclinis* F. v. Mueller, 1857)	C	16	Austr.
Actinostrobus Miquel, 1845	C	3	Austr.
Neocallitropsis Florin, 1931	C	1	N. Caled.
Fitzroya J. D. Hooker, 1851	C	1	Chile
Diselma J. D. Hooker, 1857	C	1	Tasm.
Widdringtonia Endlicher, 1847	C	3	S.Afr.
Tetraclinis Masters, 1892	C	1	N.Afr.
Libocedrus Endlicher, 1847 (incl. *Papuacedrus* Li, 1953; *Pilgerodendron* Florin, 1930)	C	9	S.Pac.
Austrocedrus Florin & Boutelje, 1954	C	1	Chile
Subtribe 5			
Taxodium Richard, 1810	T	2	N.Amer.
Glyptostrobus Endlicher, 1847	T	1	China
Tribe Cryptomerieae Vierhapper, 1910			
Cryptomeria D. Don, 1841	T	1	E.Asia
Tribe Cunninghamieae Zuccarini, 1842			
Subtribe 1			
Cunninghamia R. Brown, 1826	T	2	China
Taiwania Hayata, 1906	T	1	China
Subtribe 2			
Athrotaxis D. Don, 1841	T	3	Tasm.

group of cupressaceous genera, with or without addition of some taxodiaceous genera, forms a taxon coordinate with a second taxon comprising araucarians, abietineans, and some or all taxodiaceous genera.

The great surge of interest in gymnosperms at the turn of the twentieth century resulted in investigations of the life histories of several genera. Many of these investigations were accompanied by phylogenetic speculations, and Saxton (1913) went so far as to base his classification entirely on characters of gametophyte and embryogeny, which, a priori, he considered most important. Virtually alone among twentieth century authors, he considered separation of taxodiaceous and cupressaceous genera on the basis of phyllotaxis untenable and included them in a single family Cupressaceae, with rather different subgroupings than those proposed here (Table 1). His taxonomic system has been ignored by later workers, probably as a result of his extreme insistence on the unreliability of external characters. Lotsy (1911), in contrast, partially using the same evidence, divided conifers into two fundamentally divergent lines, placed the cupressaceous genera in his "Florales", and divided the taxodiaceous genera about equally between "Florales" and "Inflorescentiales" on the basis of degree of reduction of gametophytes. Much later, on the basis of wood characters, Greguss (1955) also segregated taxodiaceous and cupressaceous genera into widely separated groups. Neither of these attempts to recognize fundamental higher order differences between taxodiaceous and cupressaceous genera on the basis of restricted criteria has had any more acceptance than Saxton's emphasis on characteristics of gametophytes and embryogeny.

Besides segregating these genera into widely separated taxa Lotsy (1911) also treated them as representatives of five rather than the usual two families [Sequoiaceae, Cupressaceae, Actinostrobaceae, Juniperaceae, and Taxodineen (sic)]. Familial segregation culminated in the work of Hayata (1931, 1932). In addition to the families recognized, but not formally described, by Lotsy, Hayata proposed six additional segregates, Sciadopityaceae, Limnopityaceae (an alternative name for Taxodiaceae, restricted by him to *Taxodium* and *Glyptostrobus*), Cryptomeriaceae, Taiwaniaceae, Cunninghamiaceae, and Tetraclinaceae. Of these segregates, only Sciadopityaceae, restricted to the distinctive Japanese umbrella pine (*Sciadopitys verticillata*), has achieved occasional acceptance by subsequent authors. While most conifer taxonomists have been unwilling to accept numerous segregate families from among the taxodiaceous and cupressaceous genera, as late as 1948 Hu and Cheng assigned the newly discovered *Metasequoia glyptostroboides* to a monotypic Metasequoiaceae because its decussate phyllotaxis bridged the traditional gap between taxodiaceous and cupressaceous genera. Later authors have recognized *Metasequoia* as an unquestionably taxodiaceous genus, but Hu's and Cheng's contention of morphological intermediacy cannot be lightly dismissed.

Another factor contributing to continued recognition of separate families for taxodiaceous and cupressaceous genera has been a general trend toward generic segregation among conifers. This proliferation has been most notable in Podocarpaceae, where the large genus *Podocarpus* has recently been divided into several genera along old sectional lines (de Laubenfels, 1969; 1972) and in Cupressaceae s. s., with the fragmentation of *Libocedrus* (Florin, 1930; Florin and Boutelje, 1954; Kurz, 1873; Li, 1953a) and other genera. Among taxodiaceous genera, which comprise only fourteen species, this trend has been much less marked, and in this century only one segregate genus (*Sequoiadendron*) has been proposed for a previously known species (Buchholz, 1939). In contrast to the general acceptance of narrow generic concepts for cupressaceous genera, the validity of generic segregation of the redwoods was a subject of keen debate (Dayton, 1943; Doyle, 1945a), and even *Metasequoia* has been merged with *Sequoia* (Schwarz and Weide, 1962). The large number of cupressaceous genera often recognized has contributed to resistance to their merger in a single family with the smaller number of morphologically more diverse taxodiaceous genera. Generic multiplication has also resulted in hierarchical inflation for groupings of cupressaceous genera, as in Li's (1953a) classification, which distributes these genera among six tribes in two subfamilies, while Hida (1962) accepted only four suprageneric groups of taxodiaceous genera.

These diverse treatments of a group of genera currently recognized as being closely allied are not simply a result of ignorance on the part of our predecessors but are also a result of the complicated and rather obscure pattern of relationships displayed by relictual groups. Taxodiaceous genera are usually regarded as such a group of scattered Tertiary relicts, devoid of progressive elements, while Cupressaceae s. s., like Pinaceae and Podocarpaceae, is viewed as a more vigorous and successful group (de Laubenfels, 1965). The familial realignment proposed here (Table 1) suggests that cupressaceous genera are, in fact, the otherwise missing progressive elements of "Taxodiaceae" that have resisted Neogene climatic desiccation by adoption of scale leaves.

Materials and Methods

I have approached the two parts of this study, comparisons of taxa at familial and generic levels, with the same set of methods. In a study at these levels, genetic evidence of relationship is lacking and the best available measure of relatedness is overall similarity of features between two taxa. One factor that has inhibited past discussion of relationships among conifers is the wide scattering of published comparative data. I have assembled here distributions of character states for all characters for which I could obtain comparable data for Pilger's six conifer families (Tables 2 and 3) and for all taxodiaceous genera as well as *Callitris* and

TABLE 2. LIST OF CHARACTERS OF CONIFERS AND THEIR PREDOMINANT CHARACTER STATES.

1. Phyllotaxis: 1. spiral, 2. opposite, 3. whorled, 4. spirals of opposite pairs. **2.** Ontogenetic sequence of leaf types: 1. flattened linear → quadrangular → quadrangular, 2. flattened linear → flattened linear or scale → flattened linear or scale, 3. flattened linear → quadrangular → multiveined, 4. scale → flattened linear → flattened linear, 5. scale → multiveined → multiveined. **3.** Mature leaf form: 1. agathoid, 2. taxoid, 3. cupressoid, 4. cryptomeroid, 5. pinoid. **4.** Unit of foliar dehiscence: 1. lateral shoot systems, 2. individual leaves. **5.** Haploid chromosome number: 9–13, 15, 17–19. **6.** Mycorrhizal association: 1. endotrophic, 2. ectotrophic, 3. nodular. **7.** Branching: 1. verticillate, 2. L-shaped, 3. ascending. **8.** Bark: 1. smooth, 2. fibrous, 3. plates. **9.** Crossfield pitting in secondary xylem: 1. podocarpoid, 2. dacrydioid, 3. araucarioid, 4. cupressoid, 5. piceoid, 6. taxodioid, 7. pinoid, 8. glyptostroboid..

10. Tangential wall of ray parenchyma cells in secondary xylem: 1. smooth, 2. sievelike, 3. scalariform. **11.** Resin ducts in secondary xylem: 1. absent, 2. present. **12.** Ray tracheids in secondary xylem: 1. absent, 2. present. **13.** Biflavonoid series: 1. amentoflavone, 2. hinokiflavone, 3. cupressuflavone, 4. agathisflavone, 5. dihydrobiflavonoids, 6. none. **14.** Cyclitols: 1. sequoyitol, 2. pinitol. **15.** Sieve-element plastids: 1. starch-containing, 2. starch- and protein-containing. **16.** Estolide wax: 1. absent, 2. present. **17.** Arrangement of microsporangiate strobili: 1. solitary, 2. spicate, 3. otherwise grouped. **18.** Position of microsporangiate strobili on shoot system: 1. lateral, 2. terminal. **19.** Orientation of microsporangia on microsporophyll: 1. appressed, 2. projecting, 3. pendent.

20. Number of microsporangia per microsporophyll: 2–15. **21.** Pollen form: 1. saccate, 2. spheroidal. **22.** Pollen aperture: 1. analept, 2. atreme, 3. microlept, 4. papillate leptoma. **23.** Development of male gametophyte: 1. araucarian, 2. taxodian, 3. abietinean. **24.** Division of generative cell in male gametophyte: 1. anticlinal, 2. periclinal, 3. periclinal inverted, 4. divides within pollen tubes. **25.** Male gametes: 1. equal, 2. unequal. **26.** Degree of fusion of ovuliferous scale with bract: 1. completely free, 2. nearly free, 3. considerably fused, 4. completely fused. **27.** Number of ovules per ovuliferous scale: 1–20. **28.** Ovule orientation: 1. erect, 2. inverted. **29.** Texture of ovuliferous scale: 1. woody, 2. fleshy.

30. Number of seed wings: 0–3. **31.** Seed storage product: 1. starch, 2. lipid. **32.** Grouping of archegonia in female gametophyte: 1. solitary, 2. in a ring, 3. in complexes. **33.** Position of archegonia: 1. micropylar, 2. lateral. **34.** Number of neck cells of archegonium: 2–15. **35.** Number of tiers of neck cells: 1–4. **36.** Ventral canal cell of archegonium: 1. absent or ephemeral, 2. present. **37.** Archegonial jacket: 1. absent or weakly developed, 2. well developed, 3. common to several archegonia. **38.** Number of free nuclear divisions of proembryo: 0–6. **39.** Number of cell tiers in proembryo before suspensor elongation: 2(central mass with peripheral jacket)–4.

40. Equality of proembryonal tiers: 1. equal, 2. unequal. **41.** Types of embryonic suspensor: 1. prosuspensor, 2. primary suspensor, 3. secondary suspensor, 4. upper jacket cells. **42.** Embryonic cap: 1. absent, 2. lower jacket cells, 3. 1–2 cells. **43.** Accessory embryos: 1. absent, 2. above prosuspensor tier, 3. prosuspensor tier, 4. rosette or primary suspensor tiers, 5. embryonic. **44.** Cleavage polyembryony: 1. absent, 2. present. **45.** Number of cotyledons: 2–18. **46.** Number of vascular traces in cotyledons: 1–2.

Cupressus (taken respectively as generalized representatives of the southern and northern hemisphere cupressaceous lines; Tables 5 and 6). This information has come primarily from reviews cited in the first paragraph of this paper, supplemented by additional published accounts

TABLE 3. CHARACTERISTICS OF CONIFER FAMILIES USING CHARACTERS AND THEIR STATES AS LISTED IN TABLE 2. This table was compiled using the following references in addition to personal observations: Behnke (1974), de Laubenfels (1953; 1962), G. Erdtman (1957; 1965), Greguss (1955), Hegnauer (1962), Khoshoo (1961), Kindl and Hoffmann-Ostenhof (1966), Locksley (1973), Maheshwari and Singh (1967), Roy Chowdhury (1962), Sporne (1965), Sterling (1963). Character states in parentheses are rare in a family, often confined to a single genus.

PODOCARPACEAE: **1**:1,2; **2**:1,2; **3**:1–4; **4**:1; **5**:9–13,15,17–19; **6**:1; **7**:1,3; **8**:1,2; **9**:1,2; **10**:1; **11**:1; **12**:1; **13**:1,(2); **14**:1; **15**:1; **16**:1; **17**:1,2; **18**:1,2; **19**:1; **20**:2; **21**:1; **22**:1; **23**:1; **24**:1; **25**:1,2; **26**:1–4; **27**:1; **28**:1,2; **29**:(1),2; **30**:0; **31**:1; **32**:1,(3); **33**:1; **34**:4–15; **35**:1; **36**:2; **37**:2; **38**:4–5; **39**:3; **40**:2; **41**:1,3; **42**:3; **43**:2; **44**:1,2; **45**:2; **46**:2.

ARAUCARIACEAE: **1**:1,2,4; **2**:3,5; **3**:1,2,4; **4**:1; **5**:13; **6**:3; **7**:1; **8**:1; **9**:3; **10**:1; **11**:1; **12**:1; **13**:1–4; **14**:1; **15**:1; **16**:?; **17**:1; **18**:1,2; **19**:2; **20**:5–15; **21**:2; **22**:1,2; **23**:1; **24**:1; **25**:1; **26**:4; **27**:1; **28**:2; **29**:1; **30**:0,2; **31**:1; **32**:2; **33**:1; **34**:12; **35**:1; **36**:1; **37**:2; **38**:5–6; **39**:2; **40**:2; **41**:3,4; **42**:2; **43**:1; **44**:1; **45**:2,4; **46**:1,2.

CEPHALOTAXACEAE: **1**:4; **2**:4; **3**:2; **4**:1; **5**:12; **6**:2; **7**:1; **8**:2; **9**:4; **10**:1,(2); **11**:1; **12**:1; **13**:1; **14**:1,2; **15**:1; **16**:1; **17**:2; **18**:1; **19**:3; **20**:2,3; **21**:2; **22**:3,4; **23**:2; **24**:4; **25**:2; **26**:1; **27**:2; **28**:1; **29**:2; **30**:0; **31**:1,2; **32**:1; **33**:1; **34**:2–5; **35**:1; **36**:1; **37**:1; **38**:4; **39**:3; **40**:2; **41**:1,3; **42**:3; **43**:3; **44**:1; **45**:2; **46**:2.

PINACEAE: **1**:1,(3); **2**:1,2; **3**:5; **4**:(1),2; **5**:12,(13); **6**:2; **7**:1,(2); **8**:3; **9**:5–7; **10**:(1),2,(3); **11**:1,2; **12**:1,2; **13**:6; **14**:1,2; **15**:2; **16**:2; **17**:1,2; **18**:1,2; **19**:1; **20**:2; **21**:1,2; **22**:1; **23**:3; **24**:2; **25**:2; **26**:2; **27**:2; **28**:2; **29**:1; **30**:1; **31**:2; **32**:1; **33**:1; **34**:4–8; **35**:2–4; **36**:2; **37**:2; **38**:3; **39**:4; **40**:1; **41**:2,3; **42**:1; **43**:4; **44**:1,2; **45**:3–18; **46**:1,2.

"TAXODIACEAE": **1**:1–(3); **2**:1,2; **3**:2–5; **4**:1,(2); **5**:(10),11; **6**:2; **7**:1,2; **8**:2; **9**:4,6,8; **10**:1,2; **11**:1,(2); **12**:1,2; **13**:1,2,5; **14**:1,2; **15**:1; **16**:1,2; **17**:1–3; **18**:1,2; **19**:2,3; **20**:2–9; **21**:2; **22**:3,4; **23**:2; **24**:1–4; **25**:1; **26**:3,4; **27**:2–9; **28**:1,2; **29**:1; **30**:0–3; **31**:2; **32**:1–3; **33**:1,2; **34**:2–4; **35**:1; **36**:2; **37**:1–3; **38**:0–5; **39**;3–4; **40**:1,2; **41**:1–3; **42**:1; **43**:2,5; **44**:1,2; **45**:2–6; **46**:2.

CUPRESSACEAE S. S.: **1**:(1)–3; **2**:2; **3**:3,4; **4**:1; **5**:11; **6**:2; **7**:1,2; **8**:2; **9**:4,6; **10**:1–3; **11**:1; **12**:1,2; **13**:1–(3); **14**:1,2; **15**:1; **16**:2; **17**:1; **18**:2; **19**:3; **20**:(2)–6; **21**:2; **22**:3,4; **23**:2; **24**:2; **25**:1; **26**:4; **27**:(1–2)–20; **28**:1; **29**:1,(2); **30**:0–3; **31**:2; **32**:3; **33**:1,2; **34**:4; **35**:1; **36**:2; **37**:2,3; **38**:2–3; **39**:3; **40**:1,2; **41**:1–3; **42**:1; **43**:5; **44**:2; **45**:2–4; **46**:2.

(cited in Tables 3 and 6), and by examination of herbarium specimens in UC and of living plants in the collections cited in Acknowledgments. Further supplementary information was gathered during visits to natural populations of all genera of Cupressaceae s. l. native to North America, and in the course of an unpublished investigation of flavonoid constituents of all taxodiaceous genera and several cupressaceous genera (including *Cupressus*) conducted at Reed College, Portland, Oregon. The data were initially assembled in two descriptive charts (one for families and one for genera) arranged as character by taxon matrices. These charts were adapted for publication by assigning numbers to each character and character state (Tables 2 and 5) and then using these numbers in constructing character profiles for each family (Table 3) or genus (Table 6). Using the original data matrices, I tallied all similarities and differences for each pair of families and genera. I then divided similarities within each pair by the total number of similarities and dissimilarities between their constituents and multiplied by 100 to

obtain percent similarity values for pairs of families (Table 4) and genera (Table 7). The total number of comparisons for a pair is usually greater than the number of characters listed (Tables 2 and 5) because most families and genera display multiple or continuous character states for at least some characters. While not all characters are equally reflective of degree of relationship between taxa, the use of a wide array of characters helps to bypass any bias that might be introduced by equal weighting of a few characters. The likelihood of spurious indications of close relationship (as measured by high similarity values) resulting from convergence or coincidence decreases markedly with inclusion of increasing number of phases of the biology of the taxa involved (Sneath and Sokal, 1973).

The new classification of Cupressaceae s. l. proposed here (Table 1) is based primarily on the traditional criteria of morphology and development of megasporangiate strobili. On the whole, this complex of characters has provided a satisfactory and stable basis for classification of conifers. These features have been supplemented by indications from many of the other characters examined here, including vegetative characters. I consider the tribal groups rather definite, though *Athrotaxis* might perhaps be transferred to a monotypic tribe. These tribes are nearly equivalent to the subfamilies of Hida (1962) with the addition of cupressaceous genera. I am less certain of arrangement of genera within Cupresseae, which is by far the largest tribe with 4/5 of the genera in the family. Until lineages of cupressaceous genera are better understood, it seems wise to avoid formal nomenclatural recognition of the subtribal groups proposed here. Legitimate names are available for all other suprageneric groups I recognize (Table 1). For convenience, I refer throughout this paper to taxodiaceous and cupressaceous genera, terms that do not refer to taxonomically equivalent groups of genera but rather to the usual assignment of these genera to families.

Familial Characteristics

Similarity Values. Examination of a range of characters, taken from all phases of the conifer life cycle (Table 2), shows close overall agreement in these features (including such superficial characteristics as bark form and branching pattern, as well as the traditionally more

Table 4. Percentage Similarities of Conifer Families. Coefficients were calculated by dividing similarities by total number of comparisons (in parentheses) for each pair.

Podocarpaceae					
59(59)	Araucariaceae				
59(51)	40(53)	Cephalotaxaceae			
46(56)	31(58)	29(58)	Pinaceae		
52(77)	42(77)	45(74)	47(79)	"Taxodiaceae"	
46(63)	36(64)	41(59)	42(65)	90(73)	Cupressaceae s. s.

TABLE 5. LIST OF CHARACTERS AND CHARACTER STATES OF CUPRESSUS, CALLITRIS, AND TAXODIACEOUS GENRA.

1. Mature phyllotaxis: 1. spiral, 2. opposite, 3. whorls of three, 4. verticillate. **2.** Ontogenetic sequence of leaf types: 1. flattened linear → quadrangular → quadrangular or scale, 2. flattened linear → flattened linear or scale → flattened linear or scale, 3. flattened linear → cladodes and scales → cladodes and scales. **3.** Mature leaf types: 1. cupressoid, 2. cryptomeroid, 3. taxoid, 4. pinoid, 5. athrotaxoid, 6. "cladodes". **4.** Stomatal distribution on leaves: 1. hypostomatic, 2. amphistomatic, 3. epistomatic. **5.** Orientation of stomata: 1. longitudinal, 2. diverse, 3. transverse. **6.** Stomatal papillae: 1. absent, 2. rare, 3. numerous. **7.** Number of stomatal subsidiary cells: 4–16. **8.** Cycles of stomatal subsidiary cells: 1. monocyclic, 2. weakly bicyclic, 3. bicyclic, 4. weakly tricyclic. **9.** Sharing of subsidiary cells by adjacent stomatal apparatuses: 1. never, 2. occasionally, 3. often.

10. Shoot persistence: 1. annually deciduous, 2. semi-deciduous, 3. evergreen. **11.** Haploid chromosome number: 10–11. **12.** Growth rings in secondary xylem: 1. indistinct, 2. distinct. **13.** Cross-sectional shape of tracheids in secondary xylem: 1. squarish, 2. rounded. **14.** Average radial diameter (μm) of tracheids: 11.2–33.4. **15.** Longitudinal resin ducts in secondary xylem: 1. absent, 2. rare, 3. regular. **16.** Longitudinal parenchyma in secondary xylem: 1. absent, 2. present. **17.** Rays per square mm of tangential surface of secondary xylem: 15–180. **18.** Ray height (cells) in secondary xylem: 1–60. **19.** Ray width (cells): 1–2.

20. Pit diameter (μm) on tangential wall of tracheids in secondary xylem: 5–21. **21.** Types of crossfield pits in secondary xylem: 1. podocarpoid, 2. dacrydioid, 3. taxodioid, 4. cupressoid, 5. glyptostroboid, 6. piceoid. **22.** Number of pits in crossfield: 1–8. **23.** Ray tracheids in secondary xylem: 1. absent, 2. occasional. **24.** Horizontal walls of wood parenchyma: 1. smooth, 2. thickened or nodular. **25.** Horizontal walls of ray cells: 1. smooth, 2. coarse, 3. pitted. **26.** Tangential walls of ray cells: 1. smooth, 2. nodular. **27.** Biflavonoid series: 1. amentoflavone, 2. hinokiflavone, 3. cupressuflavone, 4. dihydrobiflavonoids. **28.** Leaf wax: 1. nonestolide, 2. estolide. **29.** Tropolones: 1. absent, 2. present.

30. Sesquiterpene series: 1. cedrane, 2. humulane, 3. thujopsane, 4. cuparane, 5. selinane, 6. guaiane, 7. cadinane, 8. caryophyllane. **31.** Glycoflavonoids: 1. absent, 2. present. **32.** Arrangement of microsporangiate strobili: 1. solitary, 2. spicate, 3. aments, 4. whorled. **33.** Number of microsporangia per microsporophyll: 2–10. **34.** Leptoma of pollen grain: 1. smooth, 2. pouting, 3. papillate. **35.** Shape of ovuliferous cone scale: 1. peltate, 2. elongate, 3. flattened, 4. triangular. **36.** Number of seed wings: 0–3. **37.** Ovules per ovuliferous scale: 1–20. **38.** Ovule orientation: 1. erect, 2. inverted. **39.** Arrangement of megaspores after meiosis: 1. linear, 2. various, 3. T-shaped.

40. Grouping of archegonia in megagametophyte: 1. solitary, 2. in a ring, 3. in complexes. **41.** Position of archegonia: 1. micropylar, 2. lateral. **42.** Structure of young megagametophyte: 1. single layer, 2. upper part single, lower part double or massive, 3. double layer. **43.** Archegonial jacket: 1. scattered cells, 2. single layer, uninucleate, 3. single layer, partly binucleate, 4. multiple layers, 5. absent. **44.** Number of embryonic free nuclear divisions: 0–5. **45.** Number of cells in E-tier of proembryo: 1–20. **46.** Upper tier of proembryo: 1. absent, 2. open, 3. partly closed, 4. closed. **47.** Primary embryonic suspensor: 1. absent, 2. present. **48.** Cleavage of polyembryony: 1. absent, 2. present. **49.** Number of cotyledons: 2–9.

important reproductive and anatomical characters) between taxodiaceous and cupressaceous genera (Table 3), much as other coniferous families have distinctive character assemblages. The magnitude of this

TABLE 6. CHARACTERIZATION OF CUPRESSUS, CALLITRIS, AND TAXODIACEOUS GENERA USING CHARACTERS AND THEIR STATES AS LISTED IN TABLE 5. This table was compiled using the following references in addition to personal observations: Butts and Buchholz (1940), de Laubenfels (1953; 1962), Dogra (1967), H. Erdtman and Norin (1966), Florin (1930; 1952), Gaussen (1944–1974), Geiger and Buck (1973), Geiger and de Groot-Pfleiderer (1973), Greguss (1955; 1972), Khoshoo (1961), Locksley (1972), Maheshwari and Singh (1967), Niemann and Miller (1975), Roy Chowdhury (1962), Wang and Chien (1964). Character states in parentheses are uncommon conditions or extremes. Double parentheses indicate extremely rare character states. A dash indicates inapplicability of a character to a genus.

Sciadopitys: **1**:1,4; **2**:3; **3**:1,6; **4**:1; **5**:1; **6**:3; **7**:8; **8**:1; **9**:1; **10**:3; **11**:10; **12**:2; **13**:1; **14**:22.4; **15**:1; **16**:1; **17**:32–35; **18**:1–7(10); **19**:1; **20**:8–9; **21**:1,2; **22**:1(2); **23**:1; **24**:—; **25**:1; **26**:1; **27**:1,2; **28**:1; **29**:1; **30**:1; **31**:1; **32**:2; **33**:2; **34**:1; **35**:2; **36**:2; **37**:5–9; **38**:2; **39**:1; **40**:1; **41**:1; **42**:1; **43**:2; **44**:5; **45**:12–20; **46**:3; **47**:1; **48**:2; **49**:2(4).

Sequoia: **1**:1; **2**:2; **3**:1–3; **4**:2; **5**:2; **6**:1; **7**:4–5(10); **8**:3; **9**:1; **10**:3; **11**:33; **12**:(1),2; **13**:1,(2); **14**:29.5; **15**:3; **16**:2; **17**:30–40; **18**:1–20(30); **19**:1(2); **20**:14–16; **21**:3,(1,4,5); **22**:1–3(5); **23**:2; **24**:1,2; **25**:1,(3); **26**:1,(2); **27**:1; **28**:2; **29**:?; **30**:?; **31**:2; **32**:1; **33**:2–5; **34**:1,3; **35**:1; **36**:2; **37**:5–7; **38**:2; **39**:2; **40**:3; **41**:2; **42**:2; **43**:1; **44**:0; **45**:4; **46**:1; **47**:2; **48**:2; **49**:2.

Sequoiadendron: **1**:1; **2**:1; **3**:1,2; **4**:2; **5**:2; **6**:2; **7**:4–6(12); **8**:3; **9**:1; **10**:3; **11**:11; **12**:2; **13**:1,(2); **14**:21.3; **15**:3; **16**:2; **17**:40–45; **18**:1–12(30); **19**:1(2); **20**:11–13; **21**:3,(1,4,5); **22**:1–2(6); **23**:2; **24**:1,2; **25**:1,(3); **26**:1; **27**1,2; **28**:?; **29**:?; **30**:?; **31**:1; **32**:1; **33**:(2)3(5); **34**:1,3; **35**:1; **36**:2; **37**:3–9; **38**:2; **39**:1; **40**:3; **41**:2; **42**:1; **43**:1; **44**:3; **45**:2–3; **46**:3; **47**:1; **48**:2; **49**:(2)–(6).

Metasequoia: **1**:2; **2**:2; **3**:4; **4**:2; **5**:1; **6**:3; **7**:4–10(12); **8**:2; **9**:1; **10**:1; **11**:11; **12**:2; **13**:1; **14**:27.8; **15**:2; **16**:2; **17**:45–50; **18**:1–16(20); **19**:1(2); **20**:9–10(13); **21**:3,(4,5); **22**:1–2(4); **23**:2; **24**:1?,2; **25**:1–3; **26**:(1),2; **27**:1,2,4; **28**:1; **29**:?; **30**:?; **31**:1; **32**:3; **33**:(2)5–8(9); **34**:1,2; **35**:1; **36**:2; **37**:5–8; **38**:2; **39**:1; **40**:3; **41**:1,(2); **42**:1; **43**:2; **44**:3; **45**:2–4; **46**:2; **47**:2; **48**:2; **49**:2.

Cupressus: **1**:2; **2**:2; **3**:1; **4**:2; **5**:1; **6**:3; **7**:4–6(7); **8**:2; **9**:3; **10**:3; **11**:11; **12**:1,2; **13**:1,(2); **14**:12.1–32.0; **15**:2; **16**:2; **17**:65–180;**18**:1–12(30); **19**:1,((2)); **20**:6–13; **21**:4; **22**:1–3(5); **23**:1; **24**:1,2; **25**:3; **26**:1,2; **27**:1–3; **28**:?; **29**:2; **30**:1–4; **31**:1; **32**:1; **33**:3–10; **34**:1; **35**:1; **36**:2; **37**:3–20; **38**:1; **39**:1; **40**:3; **41**:1; **42**:1; **43**:2; **44**:2–3; **45**:2–4; **46**:2; **47**:2; **48**:2; **49**:(2)–(5).

Callitris: **1**:3; **2**:2; **3**:1; **4**:2; **5**:1; **6**:2; **7**:4–6(10); **8**:2; **9**:3; **10**:3; **11**:11; **12**:1,2; **13**:(1),2; **14**:11.2–33.4; **15**:3; **16**:2; **17**:15–120; **18**:1–10(25); **19**:1,((2)); **20**:5–21; **21**:(1),4,6; **22**:1–2(4); **23**:1; **24**:1; **25**:1,((3)); **26**:1; **27**:2; **28**:2; **29**:1; **30**:5,6; **31**:1; **32**:1,(2); **33**:2–4; **34**:1; **35**:4; **36**:1–30; **37**:2–8; **38**:1; **39**:1; **40**:3; **41**:2; **42**:3; **43**:2; **44**:2; **45**:4; **46**:4; **47**:2; **48**:2; **49**:2.

Taxodium: **1**:1; **2**:2; **3**:1,3; **4**:2; **5**:3; **6**:1; **7**:4–8(16); **8**:3; **9**:2; **10**:1,2; **11**:11; **12**:(1),2; **13**:1; **14**: 20.9–31.6; **15**:2; **16**:2; **17**:50–80; **18**:1–24(60); **19**:1,((2)); **20**:8.5–11.0; **21**:3,(1,4,5); **22**:1–4(8); **23**:1; **24**:1; **25**:1,3; **26**:1; **27**:1,2; **28**:1; **29**:1; **30**:5; **31**:1; **32**:3; **33**:(3)4–5(9); **34**:1,2; **35**:1; **36**:0; **37**:2; **38**:1; **39**:1; **40**:3; **41**:1; **42**:1; **43**:3; **44**:3; **45**:2–3; **46**:2; **47**:1; **48**:2; **49**:(2)–(9).

Glyptostrobus: **1**:1; **2**:1; **3**:1–3; **4**:2; **5**:1; **6**:1; **7**:4–6(13); **8**:4; **9**:1; **10**:2; **11**:11; **12**:2; **13**:1; **14**:21.3; **15**:2; **16**:2; **17**:85–90; **18**:1–18(30); **19**:1(2); **20**:10–11; **21**:(3,4),5; **22**:1–4; **23**:1; **24**:1; **25**:2,3; **26**:1; **27**:2; **28**:1; **29**:?; **30**:?; **31**:1; **32**:1; **33**:2; **34**:1,2; **35**:2; **36**:1; **37**:2; **38**:2; **39**:1; **40**:3; **41**:1; **42**:1; **43**:?; **44**:3; **45**:4; **46**:2; **47**:1; **48**:2; **49**:3–4.

Cryptomeria: **1**:1; **2**:1; **3**:2; **4**:2; **5**:2; **6**:1; **7**:4–6(12); **8**:3; **9**:2; **10**:3; **11**:11; **12**:2; **13**:1; **14**:16.7; **15**:2; **16**:2; **17**:40–45; **18**:1–20(24); **19**:1(2); **20**:9–12; **21**:(3,4),5; **22**:1–2(5); **23**:1; **24**:1; **25**:1,2; **26**:1; **27**:1,2; **28**:2; **29**:1; **30**:5,7; **31**:1; **32**:2; **33**:(3)–(5); **34**:3; **35**:2; **36**:0(3); **37**:2–6; **38**:1; **39**:1; **40**:3; **41**:1; **42**:1; **43**:4; **44**:3; **45**:2–3; **46**:3; **47**:1; **48**:2; **49**:(2)–(4).

TABLE 6. *Continued*

Cunninghamia: **1**:1; **2**:2; **3**:3; **4**:1,2; **5**:1; **6**:1; **7**:4–6(9); **8**:2; **9**:1; **10**:3; **11**:11; **12**:2; **13**:1,(2); **14**:31.8; **15**:2; **16**:2; **17**:100–105; **18**:1–7(30); **19**:1(2); **20**:6.5–11.0; **21**:1,(3),5; **22**:1–3(5); **23**:1; **24**:1; **25**:1,(2); **26**:1; **27**:1,2; **28**:2; **29**:1; **30**:1; **31**:1; **32**:4; **33**:2–4; **34**:1; **35**:3; **36**:2; **37**:3; **38**:2; **39**:1; **40**:2; **41**:1; **42**:1; **43**:3; **44**:3; **45**:2–3; **46**:2; **47**:2; **48**:2; **49**:2.

Taiwania: **1**:1; **2**:1; **3**:1,2; **4**:2; **5**:1; **6**:1; **7**:4–6(14); **8**:4; **9**:2; **10**:3; **11**:11; **12**:2; **13**:1; **14**:14.3; **15**:1; **16**:2; **17**:85–90; **18**:1–7(10); **19**:1; **20**:7–8; **21**:1,3–5; **22**:1–3(7); **23**:1; **24**:—; **25**:1; **26**:1; **27**:2; **28**:(1),2; **29**:1; **30**:1,2,5,7,8; **31**:1; **32**:1; **33**:2; **34**:1; **35**:3; **36**:2; **37**:1–2; **38**:2; **39**:?; **40**:?; **41**:?; **42**:?; **43**:4; **44**:3; **45**:2–3; **46**:4; **47**:1; **48**:2; **49**:2.

Athrotaxis: **1**:1; **2**:2; **3**:1,5; **4**:2,3; **5**:2; **6**:1; **7**:4–7; **8**:1; **9**:3; **10**:3; **11**:11; **12**:2; **13**:1; **14**:25.0; **15**:3; **16**:2; **17**:50–60; **18**:1–12(14); **19**:1(2); **20**:10–12; **21**:3; **22**:1?3(6); **23**:1; **24**:1; **25**:1,(2); **26**:1; **27**:?; **28**:?; **29**:1; **30**:1,7; **31**:1; **32**:1; **33**:2(4); **34**:2; **35**:2; **36**:2; **37**:3–6; **38**:2; **39**:3; **40**:3; **41**:2; **42**:2; **43**:5; **44**:(1)2; **45**:1; **46**:4; **47**:1; **48**:1; **49**:2.

agreement is revealed by comparisons of similarity values between pairs of families (Table 4). While Podocarpaceae, Araucariaceae, Cephalotaxaceae, and Pinaceae resemble each other in 29 to 59 percent of comparisons, and while each resembles the taxodiaceous and cupressaceous genera in 36 to 52 percent of comparisons, the cupressaceous genera share 90 percent of their character states with the taxodiaceous genera. This is about the same similarity as shown by *Pinus* to other genera of Pinaceae, some aberrant podocarps and "typical" Podocarpaceae, or *Agathis* and *Araucaria*. Resemblance of cupressaceous and taxodiaceous genera is further emphasized by examination of the five characteristics in which the former exhibit character states not found in the latter. Phyllotaxis, tangential wall of ray parenchyma cells, biflavonoid series, number of ovules per ovuliferous scale, and texture of ovuliferous scale are all characters that vary among taxodiaceous genera. Distinctive states found in cupressaceous genera (whorled phyllotaxis, scalariform walls, cupressuflavone, up to twenty ovules, and fleshy cones) are generally exaggerations of taxodiaceous trends and some are confined to single genera.

Phyllotaxis. Since separation of Cupressaceae s. s. from "Taxodiaceae" has historically been based on phyllotaxis, it is important to assess the value of this character for familial delimitation. Even without reference to the decussate leaves of *Metasequoia,* or the spiral leaves of immature plants of *Widdringtonia,* one can see that phyllotaxis (Table 3) is a poor family character. Only Cephalotaxaceae and Pinaceae have uniform phyllotaxis. The former is monotypic and the latter shows variations of spiral phyllotaxis due to differential internodal elongation. Araucariaceae and Podocarpaceae have some genera with spiral leaves and other genera with opposite leaves, and *Podocarpus* s. l. has both conditions. While Cupressaceae s. s. is the sole coniferous group that has whorls of three or four leaves at a node, most cupressaceous genera have

TABLE 7. PERCENTAGE SIMILARITY OF CUPRESSUS, CALLITRIS, AND TAXODIACEOUS GENERA. Coefficients were calculated by dividing similarities by total number of comparisons (in parentheses) for each pair.

Sciadopitys											
40(58)	*Sequoia*										
49(55)	75(59)	*Sequoiadendron*									
45(66)	62(61)	70(60)	*Metasequoia*								
39(59)	62(55)	68(56)	72(54)	*Cupressus*							
40(58)	68(59)	66(56)	60(58)	68(60)	*Callitris*						
44(59)	50(58)	66(58)	69(58)	63(56)	56(63)	*Taxodium*					
47(51)	56(55)	71(56)	66(53)	61(51)	55(56)	70(54)	*Glyptostrobus*				
45(58)	53(53)	83(54)	65(57)	62(55)	58(59)	68(57)	73(52)	*Cryptomeria*			
51(55)	62(56)	72(54)	72(54)	64(56)	54(59)	62(56)	58(48)	62(52)	*Cunninghamia*		
50(54)	50(50)	71(49)	50(52)	43(53)	50(58)	56(55)	64(45)	63(55)	55(56)	*Taiwania*	
46(50)	63(52)	66(50)	55(51)	50(54)	52(61)	51(55)	54(46)	55(49)	56(52)	55(49)	*Athrotaxis*

opposite leaves. Since the whorled condition has probably arisen independently in different lines (e.g., in *Juniperus* and the Callitroids), it is not strong evidence for familial segregation.

Leaf Form. The other major vegetative character historically used to divide taxodiaceous and cupressaceous genera into two families is leaf form (Table 3). Cupressoid and cryptomerioid scale leaves found in cupressaceous genera are also found in taxodiaceous genera, along with taxoid and pinoid leaves, among others. *Microcachrys* bears the same relation (in terms of leaf form and phyllotaxis) to the majority of Podocarpaceae that *Cupressus* does to the taxodiaceous genera. While most podocarps, like several taxodiaceous genera, have spirally arranged taxoid leaves, *Microcachrys,* like *Cupressus,* has decussate scale leaves. This has never, to my knowledge, led to a suggestion for segregation of *Microcachrys* into a separate family.

Additional Vegetative Characters. Despite variability within families and overlap between families, there is a distinctive array of vegetative features for each conifer family, including Cupressaceae s. l. Shoot organization, chromosome number, and crossfield pitting, taken together, are sufficient for distinguishing families. Cupressaceae s. l. differs from Cephalotaxaceae in phyllotaxis, from Pinaceae in abscising lateral shoot systems instead of individual leaves, from Araucariaceae and Podocarpaceae in crossfield pit-types, and from all except Podocarpaceae in chromosome number. Other character states are features of this family alone (L-shaped branching, scalariform walls of ray parenchyma cells) or are shared with some but not all other families (ontogenetic sequence of leaf types).

Reproductive Characters. In characters of microsporangiate structures (orientation and number of microsporangia on microsporophyll, microlept spheroidal pollen grains) and male gametophytes (taxodian development), taxodiaceous and cupressaceous genera show complete agreement and contrast with all families except Cephalotaxaceae, which differs (in male characters) only in having unequal male gametes. Megasporangiate characters (complete fusion of ovuliferous scale with bract, number of ovules per ovuliferous scale and their occasional erect orientation) and megagametophytic characters (archegonial complexes sometimes lateral, no more than four neck cells in archegonium) also show close overall agreement, though taxodiaceous genera tend to be more diverse than genera in other families. Archegonial complexes and structure of ovulate cone are characteristic of Cupressaceae s. l. and such cupressaceous specializations as the fleshy "berry" of *Juniperus* (associated with bird dispersal) or the relatively large number of ovules on cone scales of certain *Cupressus* species are no more unusual among taxodiaceous genera than the disintegrating cone and large seeds of *Taxodium,* which adapt it for water dispersal. The general ground plan of embryogeny (relatively few free nuclear divisions, prosuspensor, primary and secondary suspensors, and cleavage polyembryony all present) is also characteristic of Cupressaceae s. l. Such unusual features as

accessory embryos derived from the E-tier and diamond-shaped embryos are found only in taxodiaceous and cupressaceous genera.

Taxodiaceous genera are more diverse in most of these features than cupressaceous genera and this diversity includes most character states found in the latter. Cupressaceae s. l. is little more diverse than "Taxodiaceae" and is comparable in diversity to the other large families Pinaceae and Podocarpaceae. If only two or three cupressaceous genera were known, rather than eighteen, they would likely never have been separated from the taxodiaceous genera in a segregate family.

Similarities within Cupressaceae s. l.

Since cupressaceous genera are too numerous to treat all in detail here, I have chosen *Cupressus* and *Callitris* as relatively primitive representatives of the two cupressaceous subtribes (Table 1) to compare with the taxodiaceous genera in a manner analogous to the comparison of conifer families. Many characters compared for these genera (Table 5) are the same as those compared for families (Table 2), but many additional features, such as epidermal characters, are used and several features without diagnostic value within Cupressaceae (such as ectotrophic mycorrhizae, fibrous bark, presence of both sequoyitol and pinitol, and taxodian development of microgametophyte) are deleted. Character profiles for the genera (Table 6) show considerable diversity in such characters as leaf form, density of rays in secondary xylem, sesquiterpene series, and structure of megagametophyte. The most distinctive profile belongs to *Sciadopitys,* which, with its unique "cladodes", chromosome number, and other features, is morphologically isolated within Cupressaceae. The average of similarity values in comparisons of *Sciadopitys* with other genera of Cupressaceae (Table 7) is 45 percent compared with an average of 61 percent for comparisons of genera within Cupressoideae, a difference significant at $P < 0.001$. This supports its assignment to a monotypic subfamily and provides a rationale for omitting it from discussion of affinities of other genera.

Genera of Cupressoideae compared here (Table 7) seem about equally similar to each other, with values ranging mostly from 50 to 75 percent (av. 61 percent, s. d. 8.09). Genera of Cupresseae form a closely knit group with average similarity 65 percent for comparisons within the group, contrasted with 60 percent average similarity for comparisons of these genera with other genera of Cupressoideae (different at $P < 0.05$). Genera of Cunninghamieae form a much looser aggregation having an average similarity of only 55 percent with each other (different at $P < 0.05$ from the average value for comparisons within Cupresseae). Within Cupresseae, *Cupressus* has about the same high similarity to *Metasequoia* and *Sequoidadendron* as it does to *Callitris,* while the latter is as similar to *Sequoia* and *Sequoiadendron* as it is to *Cupressus* (all about 70 percent). The alignment of these cupressaceous genera with other Cupresseae is underlined by their

average similarity of 64 percent to taxodiaceous genera of this tribe, which is significantly different at $P < 0.01$ from their average similarity of 54 percent to other taxodiaceous genera.

Cupressus and *Callitris,* separately, seem to fit rather well in Cupresseae. *Cupressus* in particular, with its globular ovulate cones and peltate cone scales (Table 6), seems a close relative of *Sequoia, Sequoiadendron,* and *Metasequoia. Callitris,* while differing in these features from other Cupresseae discussed, agrees with the sequoiids in such characters as lateral archegonia and presence of stomatal papillae. *Cupressus* and *Callitris* agree in some other features common to the majority of cupressaceous genera, such as whorled phyllotaxis in seedlings, but a similar phyllotaxis occurs sporadically in taxodiaceous genera (de Laubenfels, 1953). Furthermore the two genera differ, among other characters, in the absence of tropolones in *Callitris* and in the peculiar embryogeny of the latter, which is shared with *Athrotaxis* among taxodiaceous genera (Table 6). De Laubenfels (1965) has already pointed out the taxodiaceous character of *Cupressus* on the basis of a dozen characters compared for a few taxodiaceous genera. He concluded that *Cupressus* was about equally related to *Sequoiadendron* and *Cryptomeria* (a conclusion not supported here) but he did not draw the conclusion that the cupressaceous and taxodiaceous genera should be united in a single family, despite his assertion of multiple interrelationships between them. Since *Cupressus* and *Callitris* have the same degree of similarity to the taxodiaceous genera as the latter have to each other, segregation of the cupressaceous genera as a separate family would require fragmentation of the taxodiaceous genera into several families (in the manner of Hayata, 1931; 1932) to achieve a consistent system. I prefer the alternative course of treating all as members of a single family.

Evolutionary Relationships

Fossilized remains of Cupressaceae s. l. are abundant and widespread in Mesozoic and Tertiary sediments (Florin, 1963) but taxonomy of these remains is as yet unsatisfactory. There have been a few revisions of small groups (Chaney, 1951) or for limited geographical areas (Schweitzer, 1974), but there has been no comprehensive monograph of the family, and much of the paleobotanical literature is by authors unfamiliar with the morphological range of living taxa. Since relatively few fossilized reproductive structures referable to this family are known, most records of occurrence are based on the relatively undiagnostic fragments of vegetative shoots. No adequate taxonomic framework for fossil members of this family exists and many reports of their occurrence give inadequate attention to morphological features of the remains. Thus any discussion of evolutionary relationships within Cupressaceae must be somewhat speculative. Nonetheless, careful comparisons among extant taxa and attention to some reliable fossil representatives give clues to the evolutionary trends within the family.

Specializations of cupressaceous genera of the northern hemisphere all seem derivable from an ancestral condition of globular, many-scaled ovuliferous cones, cruciate, terete branchlets, and arborescent habit. These characteristics are present in certain living species of *Cupressus* and this genus is thus similar to the probable ancestor of other genera of Cupresseae subtribe 3. Morphological features of cupressaceous genera of the southern hemisphere do not point so directly to *Cupressus* as an ancestral type. A lineage involving *Widdringtonia, Tetraclinis, Libocedrus,* and *Austrocedrus* could have originated initially from a *Cupressus*-like form by reduction to two pairs of ovuliferous cone scales, but the *Callitris-Actinostrobus-Neocallitropsis* lineage resists a similar interpretation. *Austrocedrus* and *Libocedrus,* furthermore, could be allied to the northern hemisphere *Calocedrus,* which has been considered congeneric with them (Janchen, 1950), rather than to *Widdringtonia* and *Tetraclinis.* The exact placement of these two genera must await further morphological and embryological observations, but their morphology is closely comparable to that of other cupressaceous genera. In fact, genera of Cupresseae subtribes 3 and 4 are an assemblage of diversified descendants of relatively recent ancestors, while the taxodiaceous genera mostly represent remnants of lineages, equivalent to, but smaller than, these cupressaceous lines. Relative success of cupressaceous lines can be related in part to their vegetative morphology. Their diversification may have resulted from their evolution of xeromorphic scale leaves, which allowed them to survive the increasing aridity of the Tertiary (Wolfe, 1969) better than the other, broader-leaved taxodiaceous forms. The three largest cupressaceous genera (*Cupressus, Callitris,* and *Juniperus*), which are still in a state of evolutionary diversification (as evidenced by intergradation and hybridization), have cupressoid scale leaves in most or all species. Significantly, those cupressaceous genera that have broader leaves (e.g., *Thuja, Libocedrus,* and *Fitzroya*) are morphologically specialized genera (Li, 1953a) whose secondary invasion of more mesic habitats has been associated with a re-expansion of leaf surfaces. These derivative genera have retained the phyllotactic patterns of their scale-leaved ancestors.

Scale leaves are not invariably associated with decussate or whorled leaf arrangements. All shoots of *Athrotaxis cupressoides* and mature leading shoots of other extant taxodiaceous species have spirally arranged scale leaves. Furthermore, shoots of several extinct taxodiaceous forms (some species of *Brachyphyllum, Thuites,* and *Cyparissidium*), extending back to the Jurassic (Florin, 1963), also have this arrangement. The oldest known conifer remains with decussate scale leaves are referred to *Cupressinocladus ramonensis* (Chaloner and Lorch, 1966) from the Jurassic of Israel. While the authors consider this a cupressaceous form, its reproductive structures are as yet unknown, and its stomatal characters are also shared with taxodiaceous genera. A reasonable interpretation of these facts is that various taxodiaceous lines have

experimented with either scale leaves or decussate (or whorled) phyllotaxis, or both. Two (or three) of these lines, the cupressaceous forms, have been successful and have continued and expanded to the present, while other lines became extinct or have barely persisted (e. g., *Metasequoia*).

Despite their present restricted distributions, several taxodiaceous genera of Cupresseae were much more widespread during the Tertiary (Chaney, 1951; Florin, 1963) but they never underwent adaptive radiations comparable to those of the callitroid and cupressoid lines. While some taxodiaceous and cupressaceous genera were present in the Cretaceous or earlier, most seem to have emerged in the early Tertiary and are comparable in age to many angiosperm tree genera. As a result of a probable rapid adaptive radiation of callitroid and cupressoid lines in the Upper Cretaceous and Paleogene, many of the derivative genera (such as *Thuja* and *Chamaecyparis*) coexisted with relatively unmodified taxodiaceous genera throughout much of the Tertiary. The deceptive antiquity of the cupressoid derivatives is partly an artifact of the relatively poor record of Jurassic and Cretaceous conifers everywhere except in Europe, which is probably not the center of evolution of Cupressaceae. Thus we know very little about the emergence of taxodiaceous genera, since their first records are quite similar to living taxa and do not point to their ancestry. Until we have much more Mesozoic evidence, especially of reproductive structures, we cannot more closely trace evolutionary patterns within Cupressaceae. Nothing in current paleobotanical literature, however, contradicts the notion that taxodiaceous and cupressaceous genera are members of the same family.

Taxonomic Conclusions

Since *Cupressus* and *Callitris* are as closely allied to *Sequoia, Sequoiadendron,* and *Metasequoia* as the latter are to other taxodiaceous genera, the usual assignment of the first two genera to one family and the latter three to another is phylogenetically and taxonomically unacceptable. Considering the pattern of similarities that the genera display, there seem to be two possible courses available that would result in their consistent treatment. The first would be to follow Hayata (1931, 1932) in recognizing a large number of small families that are equivalent in rank to Cupressaceae s. s. The second is to treat all the genera (with the possible exception of *Sciadopitys,* which could reasonably be assigned to a monotypic family) as members of a single family. I prefer to preserve indications of relationship within the taxonomic system. Current practice in circumscription of other conifer families also favors the conservative approach. Cupressaceae, as circumscribed here, is equivalent in diversity to Pinaceae or Podocarpaceae.

Since this is not a detailed taxonomic revision of Cupressaceae, the proposed arrangement of genera (Table 1) must be tentative. While relationships of certain genera (*Cryptomeria, Athrotaxis, Tetraclinis,*

and some other callitroid genera) are problematical, this scheme is consistent with available evidence of relationships and provides a basis for further discussion of this group of conifers.

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UPPER INTERTIDAL ALGAL ZONATION ON BODEGA HEAD, SONOMA COUNTY, CALIFORNIA

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Several workers have studied intertidal zonation of marine algae along the Pacific coast of North America. Smith (1944) published the first records of vertical algal distribution from the Pacific coast. Doty (1946) correlated critical tide factors with zonation. From Washington, Rigg and Miller (1949) reported on intertidal plant and animal zonation; they compared both exposed and semi-exposed localities in the Neah Bay area.

In this paper I examine the intertidal zonation of the more conspicuous indicator algae at two localities (exposed and semi-exposed) on Bodega Head, a small peninsula surrounding Bodega Harbor, by estimating the percent cover in 10 by 10 cm quadrats. These algae include *Gigartina agardhii, G. papillata, Iridaea* spp., *Rhodomela larix, Endocladia muricata, Bossiella plumosa, Corallina vancouverensis,* and *Pelvetiopsis limitata.*

In addition, the vertical distribution of *Petrocelis fransiscana* was studied. West (1972) stated that *Petrocelis fransiscana* may be the tetrasporophyte of *Gigartina agardhii.* I shall examine if a correlation exists in the vertical zonations of *Gigartina agardhii, G. papillata,* and *Petrocelis fransiscana.*

Materials and Methods

The study was from 1 Apr to 1 Jun 1974. Four different stations were established. Stations A, B, and D were located on the exposed, western side of Bodega Head, approximately 100 m apart. Station C (unexposed) was located on the eastern side, near the harbor entrance. The slope on all stations was approximately 30–45°, and stations A, B, and D were oriented at the same angle to incoming waves. Heights above the MLLW (0.0 m level) were measured by means of a stadia rod, chalk line, and line level. Three 0.5 by 0.5 m quadrats were randomly placed (table of random numbers) along a horizontal transect at each level; each quadrat was divided into twenty-five 10 by 10 cm subquadrats. Percent cover in each of these subquadrats was estimated for the indicator algae and *Petrocelis fransiscana. Gigartina argardhii* and *G. papillata* were grouped together. Other workers have indicated how variable these two species are in terms of growth morphology (Abbott, 1972; Jensen and Tanner, 1973). Also, Abbott (1970) has stated that *Gigartina agardhii* might be considered a form of *Gigartina papillata.* I could not always distinguish between the two plants.

Most of the Corallines and *Iridaea* spp. were small plants, especially

on the exposed side of Bodega Head. The two Corallines were grouped together since they were growing intermixed with each other. The identification of very small *Iridaea* species was exceedingly difficult, but later observations showed these plants were mainly *Iridaea flaccida.*

The mean percent cover for the seventy-five 10 by 10 cm subquadrats at each tidal level was computed. Species that had an average of less than 10 percent cover on the exposed transects were omitted from the list. If the quadrats fell on tidepools, rock crevices, or surf channels, or if the degree of exposure was different from the general pattern, the quadrats were placed as close to the original place as possible (same tidal height).

Results

The mean percent cover for the 75 subquadrats at each tidal height is presented graphically in Figures 1 and 2. Three distinct algal zones are readily recognized both in the exposed and semi-exposed stations. The *Pelvetiopsis* zone has its peak distribution between 3.2 and 4.2 m (exposed) and between 1.8 and 2.7 m (semi-exposed). The *Endocladia-Gigartina-Petrocelis* zone has its peak distribution between 2.0 and 3.6 m (exposed) and between 0.6 and 2.0 m (semi-exposed). Finally, there is a Coralline-*Iridaea* zone from 2.4 m and below (exposed), and a *Rhodomela-Iridaea* zone from 1 m and below (semi-exposed).

The mussel zone at the exposed stations (1.2–3.2 m) was replaced by a barnacle zone at the semi-exposed station (1.5–2.1 m).

Discussion

Gigartina agardhii and *G. papillata* have a bimodal distribution (figs. 1 and 2, exposed and semi-exposed). Both peaks in this distribution were composed of roughly equal amounts of the two species. Thus, the bimodal distribution is not an artifact of the "grouping" type of sampling procedure.

In exposed sites *Gigartina agardhii, G. papillata,* and *Endocladia muricata* have a similar vertical distribution (fig. 1), and most likely compete for surface area. *Endocladia muricata* reaches a maximum percent cover only 0.15 m away from the low between the two peaks representing the maximum percent cover of *Gigartina agardhii* and *G. papillata.* Both of the peaks for maximum *Gigartina agardhii* and *G. papillata* percent cover lie within areas where *Endocladia muricata* is a substantial, if not dominant, component of the zone. The bimodal *Gigartina agardhii* and *G. papillata* distribution may be due to *Endocladia muricata*'s superior adaptability, and thus competiveness, at the 2.6 m level. But between 3.5–3.8 m *Gigartina agardhii* and *G. papillata* have a larger percent cover than *Endocladia muricata.*

In the semi-exposed area, there is a comparable situation, except that the heights of the two peaks in the *Gigartina agardhii* and *G. papillata* distribution are reversed. The drop between the peaks corresponds exactly to the barnacle zone (see results).

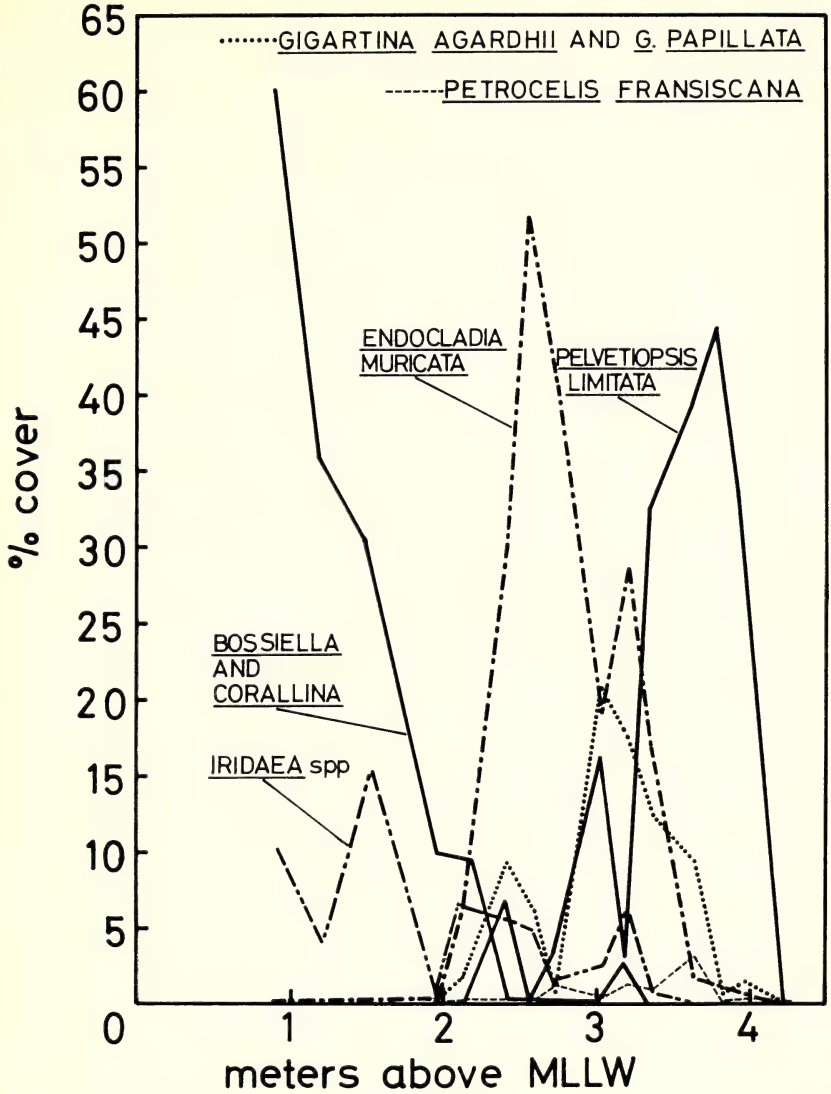

FIG. 1. Vertical distribution of algae at the exposed stations. Three zones can be recognized: the Coralline-*Iridaea* zone, the *Endocladia - Gigartina - Petrocelis* zone, and the *Pelvetiopsis* zone.

The separation of the peaks for *Pelvetiopsis limitata* and *Endocladia muricata* (exposed and semi-exposed) may indicate that ecological factors other than spatial ones determine their maximum percent cover. The overlap area may indicate that competition for space occurs at their interface.

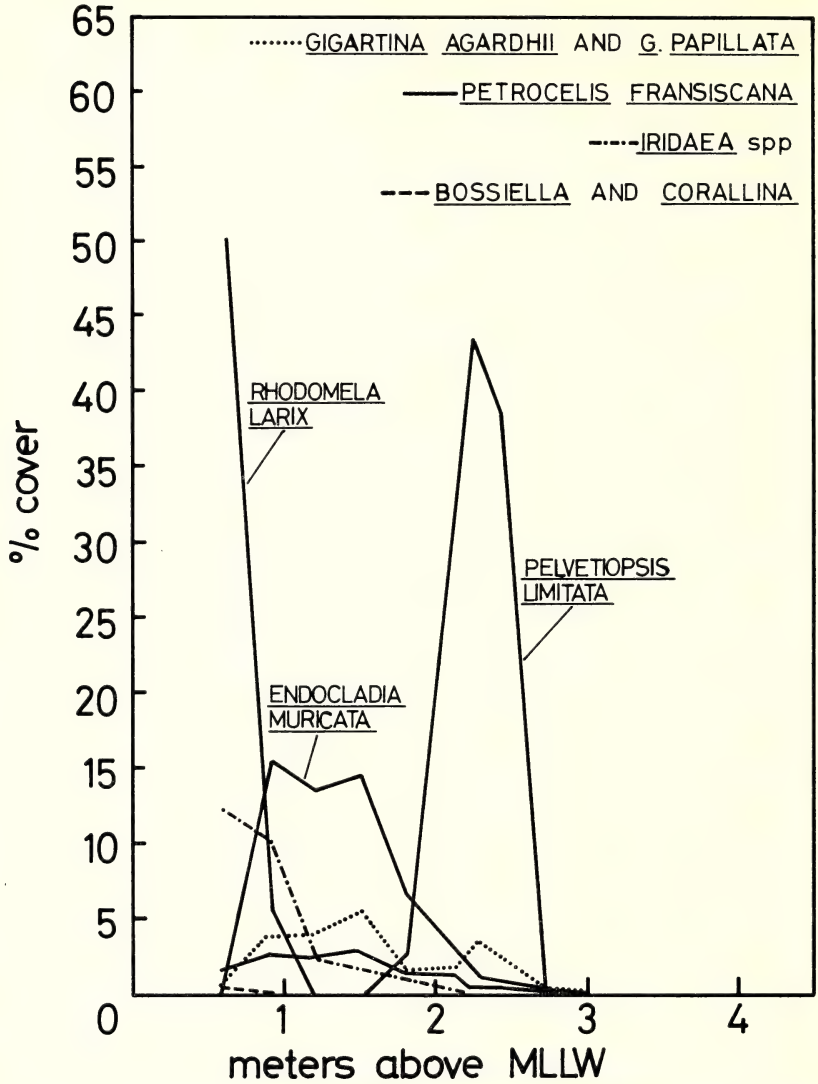

FIG. 2. Vertical distribution of algae at the semi-exposed station. Three zones can be recognized: the *Rhodomela - Iridaea* zone, the *Endocladia - Gigartina - Petrocelis* zone, and the *Pelvetiopsis* zone.

In comparing both the exposed and semi-exposed localities *Gigartina agardhii* and *G. papillata* do not form a distinct zone, but both species seem to be closely associated with *Endocladia muricata*. Other workers confirm this (Glynn, 1965; Rigg and Miller, 1949). The three plants are all resistant to desiccation and there seems to be competition for

space between *Gigartina agardhii, G. papillata,* and *Endocladia muricata.* In both exposed and semi-exposed situations, *Endocladia muricata* has a greater percent cover low in the intertidal, while *Gigartina agardhii* and *G. papillata* have a greater percent cover high in the intertidal. This agrees well with the literature, as Hinchmann (1964) found that the *G. papillata* complex was extremely resistant to desiccation.

From Figures 1 and 2, it appears that *Petrocelis fransiscana, Gigartina agardhii,* and *G. papillata* have similar distributions. This may support West's (1972) statement that *Petrocelis fransiscana* is the tetrasporophyte of *Gigartina agardhii,* although *G. agardhii* and *G. papillata* were recorded 0.30 m higher than *Petrocelis fransiscana* at the semi-exposed station, while *Petrocelis fransiscana* was found 1 m lower than *G. agardhii* and *G. papillata* at the exposed stations. *Gigartina agardhii* and *G. papillata* seem to withstand desiccation much more than *Petrocelis fransiscana.* On the exposed side of Bodega Head, *Petrocelis fransiscana* is scarce in the mussel beds, although I observed *Petrocelis* spots growing on the mussels. In general, *Petrocelis* spots found at both study localities were small, 1 to 3 cm in diameter. It appears that *Petrocelis fransiscana* is crowded out by mussels, barnacles, and other erect algae in these areas.

Glynn (1965) has pointed out how difficult it is to compare zonation studies done by different authors, even in the same locality. The vertical ranges of intertidal algae depend on several physical conditions, such as slope, degree of exposure to wave action, and surges in rock fissures.

Figure 3 compares the *Endocladia muricata* distribution from the semi-exposed station on Bodega Head with two other studies from the Pacific coast. Both Glynn (1965) and Rigg and Miller (1949) have their *Endocladia* zone almost entirely within the upper and lower limits as found on Bodega Head. Glynn (1965) found that the center of the *Endocladia-Balanus* association was 1.35 m above the MLLW, protected outer coast (fig. 3, the dark bar in the Monterey rectangle). The results from the semi-exposed station on Bodega Head agree well with his findings (fig. 3).

At Neah Bay (Rigg and Miller, 1949), the semi-exposed association was found to occur substantially higher than on Bodega Head (2.4 m vs. 1.3 m). The peak distribution of *Endocladia muricata* for exposed conditions on Bodega Head correlates well with their findings (2.6 m vs. 2.4 m). This indicates that the semi-exposed locality in the Neah Bay area is more exposed compared with the semi-exposed station on Bodega Head. The greater tidal range (about 3 m) at Neah Bay compared with Bodega Head (2.4 m) may also explain the difference.

Acknowledgments

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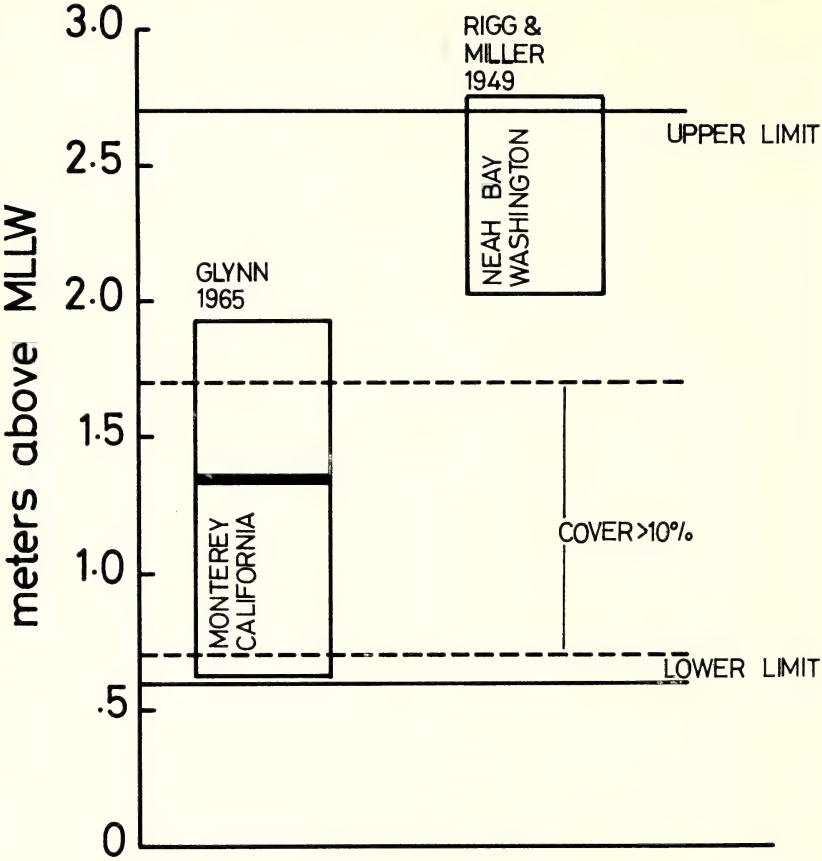

FIG. 3. Comparison of the vertical ranges of *Endocladia muricata* from the semi-exposed station on Bodega Head with the vertical ranges established by other workers for two places along the Pacific coast. The upper and lower limit lines and the two broken lines refer to Bodega Head. The dark bar in the Monterey rectangle refers to the center of the *Endocladia - Balanus* association.

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A NEW SPECIES OF PENSTEMON (SCROPHULARIACEAE) FROM MEXICO

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In collecting toward a flora of the Chihuahuan Desert region, James Henrickson and Thomas Wendt discovered the following new species, a close relative of *Penstemon barbatus* (Cav.) Roth, in the Sierra de la Madera west of Cuatro Cienegas in central Coahuila.

Penstemon henricksonii, species nova in sectione *Elmigera*; foliis basalibus ellipticis oblanceolatisve petiolatis, foliis caulinis ovatus ut in *P. cardinalibus*; floribus *P. barbato* simulantibus autem coloribus rubropurpureis vel marroninis non coccineis; loculis antherae divaricatis marginibus minute acutidentatis. Figure 1.

TYPE: Mexico, Coahuila, ca 35 (air) km west of Cuatro Cienegas in Cañon de la Hacienda in limestone, Sierra de la Madera along trail southeast of road's end, in loamy oak-pine-fir forest, 7700 to 9000 ft, 5 Aug 1973, near 27°03′ N, 102°24′ W, *J. Henrickson and T. Wendt 11903*. Holotype: RSA; Isotypes: CSLA, TEX, MEXU, NY, ARIZ, US, UC, GH.

The species is also known from a collection of fruiting material: Sierra de la Madera, among similar associates, SW Rancho Cerro de la Madera, upper Cañon del Invierno, 2500 m, 27°05′ N, 102°28′30″ W, 27 Aug 1974, *Wendt and Lott 649b*, TEX.

The name honors James Henrickson, biology professor at California State University, Los Angeles, plant anatomist, morphologist, systematist (especially of Fouquieriaceae), and student of the Chihuahuan Desert flora.

Perennial herb to 6 dm tall; stems and foliage glabrous. Basal leaves elliptic or oblanceolate, petiolate, the blades 5–12 cm long, 2–4 cm broad, petioles to 5 cm long; cauline leaves ovate to broadly lanceolate, 3–8 cm long, 2.0–3.5 cm broad, sessile, apex broadly acute; all leaves entire, glabrous, minutely punctate beneath. Inflorescence narrowly thyrsoid, bracts lanceolate, pedicels mostly 2-flowered, less than 2 cm long. Calyx segments lanceolate, acute, entire, with narrowly scarious margins, glabrous, 6–7 mm long. Corolla like that of *P. barbatus* but dark maroon-red or purplish red, the upper lip erect and shielding the anthers, lower lip sharply reflexed along throat of corolla, conspicuously bearded at base with flat, simple, yellow hairs 2 mm long; corolla 30–35 mm long, 8–10 mm broad (pressed), lower lip 10 mm long, upper somewhat longer. Anther locules opening from free tips about 4/5 of distance to common bases, divergent, glabrous; suture margins with conspicuous small sharp teeth (more than usual for *P. barbatus*). Staminode dilated distally and glabrous. Capsule ovoid-acuminate, to 15 mm long, glabrous.

Penstemon henricksonii is scattered on upper, mesic, moss-covered, north-facing slopes in a shaded oak-pine-fir forest between 2100 and 2750 m. The principal species in the forest include *Abies coahuilensis* I. M. Johnst., *Pseudotsuga menziesii* (Mirb.) Franco, *Pinus strobiformis* Engelm., *P. ponderosa* Laws. var. *arizonica* (Engelm.) Shaw, *Cupressus arizonica* Greene, and *Arbutus xalapensis* HBK., as well as several species of *Quercus* including *Q. hypoxantha* Trel., *Q. greggii* (A. DC.) Trel., and *Q. pringlei* Von Seemen. Principal shrub and herbaceous species in the forest include *Cornus stolonifera* Michx., *Holodiscus dumosa* (Nutt.) Heller, *Nolina caespitifera* Trel., *Swertia radiata* (Kell.) O. Kuntze, and species of *Stevia, Seymeria, Senecio,* and *Solanum*. The dense carpets of a goldish-green moss[*Rhytidium rugosum* (Hedw.) Kindb.] over the forest floor attest to the mesic nature of this portion of the east-west oriented Sierra de la Madera, which is frequently enshrouded by clouds during the late summer-fall rainy season.

This species differs from *P. barbatus* in having broad, ovate cauline leaves and purplish, rather than bright red, flowers. The leaves most nearly resemble those of *P. cardinalis* Woot. & Standl. of western Texas, the flowers of which differ in having very short lips and a constricted orifice.

The related *P. barbatus* ssp. *torreyi* Gray grows in the same canyon but has been collected only at elevations below 1800 m where it is infrequent along alluvial arroyo margins in a more open mesic oak-pine-madrone woodland composed of *Quercus gravesii* Sudw., *Q. glaucoides* Mart. & Gal., *Arbutus xalapensis* HBK., *Pinus ponderosa* var. *arizonica* (Engelm.) Shaw, *Fraxinus cuspidata* Torr., *Garrya ovata* ssp.

FIG. 1. *Penstemon henricksonii, sp. n.* a. habit; b, flower; c and d, anther.

lindheimeri (Torr.) Dahling, *Prunus serotina* Ehrh., *Leucania retusa* Gray, and *Dasylirion,* as well as species of *Desmodium, Abelia, Choisya, Salvia, Aquilegia, Eupatorium,* and *Eriogonum.*

I thank Ms. Frances Runyan for providing the drawing and Dr. Henrickson for data on ecological associates.

PROCEDURAL INNOVATIONS IN REVISIONARY STUDIES: COMPUTER-ASSISTED CITATION OF REPRESENTATIVE SPECIMENS

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Revisionary studies are in many ways the cornerstones of systematic botany. It is within revisions that basic relationships among specific plant groups are sketched, and it is within this framework, therefore, that most data regarding classification and evolution of plants have been documented. The importance of revisionary studies in plant systematics has been emphasized with some regularity (e.g., Robinson, 1923; Just, 1954; Stuessy, 1975).

Although presently used, time-tested methods for producing revisions have been highly successful, one wonders if, with procedural modifications, revisions could be produced more efficiently and with greater accuracy of cited information. If this were so, then the main contributions of revisionary studies to plant systematics would become even more significant, and we might come more quickly to an understanding of the diversity and interrelationships of the whole plant kingdom. This is particularly significant in view of the rapid disappearance of much of the world's flora due to the increasing size and activities of the human population.

A number of possibilities exist for procedural innovations in revisionary studies, but perhaps one of the most significant changes will come with the use of data-processing machines. The utility of a revision relates to the ease with which information can be retrieved from the revisionary framework of keys, descriptions, representative specimens, and distribution maps. The procedures involved in generating these data and presenting them in standardized formats are conceptually simple, laborious, and error-prone. It is precisely this set of attributes that is well-suited for computer application. With explicit instructions, computers can perform simple, routine tasks very rapidly and with few, if any, errors.

Although several projects already have utilized computers in procedures that relate to revisionary studies, e.g., in automatic key generation (Hall, 1970; Morse, 1971, 1974; Pankhurst, 1971, 1974; Pettigrew and Watson, 1973; Dallwitz, 1974), in automatic preparation of distribution maps (Soper, 1964, 1969; Adams, 1974), and in extracting data from floras (Keller and Crovello, 1973), none has employed the computer to produce lists of representative specimens in conventional format. Argus and Sheard (1972), Argus (1973), and Shetler et al. (1973) have used the computer to generate lists of specimens, but these are not concatenated in the standard format.

Representative specimen citations serve three important functions in revisionary studies: (1) they indicate at least some of the specimens seen or studied by the author; (2) they include information on precise locality, date of collection, and name of collector(s), which is of interest to many people, such as ecologists, floristic workers, or biographers; and (3) they serve as a convenient catalogue of identified specimens so that floristic workers or herbarium curators can refer to these data and identify duplicate material without having to write to the specialist for aid.

In our laboratory we have used computers to prepare specimen citation lists for revisionary studies on the subtribe Lagasceinae (Compositae, Heliantheae). These procedures have been helpful to our work, and we present this paper with the following specific purposes: (1) to describe a program for computer-assisted citation of representative specimens (called REVISO) and (2) to comment on the time, cost, and accuracy of using this new method with more conventional manual-file procedures. We realize that several large electronic data-processing systems such as SELGEM at the U.S. National Museum, the Generalized Information System of the now dormant Flora North America Program (Krauss 1973), the program package used by Crovello (1972) for the Greene Herbarium, or TAXIR, developed at the University of Colorado (Brill, 1971), could be modified to accomplish what we have done with REVISO (see Crovello and MacDonald, 1970, and Brenan, 1974, for a more complete index of electronic data-processing programs available). Even if this were done, however, we believe that the availability of a relatively simple, short, inexpensive program is more attractive to practicing taxonomists in their own institutions than is the prospect of time-sharing with one of the big systems (see Argus and Sheard, 1972, for a similar viewpoint).

Description of Program (REVISIO)

The REVISIO program is designed to input, manipulate, and output data consisting of label information from herbarium specimens. It is written in the PL/I optimizer language and requires 252K of storage. The types of manipulations and formats of output are determined by user-supplied control cards. The following description of the functions performed by REVISIO is intended only as a general overview.

The operation of REVISIO can be divided conceptually into three phases: data input, data manipulation, and data output. Each of these operations is discussed below.

Data Input

In the data input phase, information is read from the input file, edited to some extent, and placed in an array in storage. For most users, the input file will be a deck of cards. It is useful to examine the format of the card containing the label information in some detail, because this

will provide a good basis for understanding the operation of the program.

Each set of information from one label (hereafter called an "entry") is punched onto one or more cards. Each entry consists of six fields separated by asterisks: geography*locality*date*collector*number* herbaria*. Six asterisks must appear in each entry. The taxon designation for each of the entries is not put on the entry card itself but is provided by an additional card that precedes all entries for that taxon.

Geography.—The geography field consists of names of the political subdivisions where the specimen was collected. These names may be written in full or may be abbreviated. Full names are followed by semicolons; abbreviations, by colons. For example: US:OH:FRANKLIN CO.;*. A list of abbreviations and their full equivalents supplied to the program by the user enables the program to replace these abbreviations on output. Abbreviations do not have to be used, however, but their use can save time in data input if many specimens are from the same region.

Locality.—The specific locality is simply keypunched as it occurs on the label (often with minor editorial modifications), including brief ecological or elevational data if desired.

Date.—The date can be keypunched in several ways: 1904*; MAY 1904*; 8MAY1904*; 08 MAY 1904*; or "WITHOUT DATE"*.

Collector.—The name of the collector(s) is punched thus: MURPHY*; MURPHY ET AL.*; MURPHY & JONES*; or COLLECTOR UNKNOWN*.

Number.—The collector's number is entered in whatever form it appears on the label, consisting of numbers and/or letters, and including the use of *s.n.* when the number is not known.

Herbarium.—The last field is a list of the herbarium abbreviations (from *Index Herbariorum,* Holmgren and Keuken, 1974) separated by commas: GH, NY, F, US, OS*. The abbreviations may be input in any sequence; before data output they are sorted alphabetically.

An entire entry might look like this: US:ARI:PIMA CO.;*BABOQUIVARI MTS*16APR1935*MAGUIRE*10746*GH, NY*.

In some cases the information from the label will not fit into the various formats just described. For example, in the case of dates a range may be specified: 16–20 JAN 1895. To deal with this type of problem, REVISIO has the capability of storing one piece of information for manipulation while using the other for output. On the data card the manipulation datum is keypunched first in the date field followed by what is to be printed in quotes: 16JAN1895 "16–20 JAN 1895"*. If a sort by date is requested, this entry will be sorted with a date of 16 JAN 1895, but a listing will produce a date of 16–20 JAN 1895. This substitute option is available for three of the fields: geography, date, and number.

Taxon Name and Number.—In addition to the information on the specimen label, each entry is associated with a taxon name and its arbitrarily assigned number. This taxon information is read from the

card that precedes the entries for that taxon. The taxon name and number may be sorted during data manipulation as though they were keypunched individually for each entry.

Thus, after input, there are eight kinds of information stored for each entry, six from the label proper, plus one for the taxon name and another for an arbitrarily assigned taxon number.

Data Manipulation

During data manipulation, there are two functions available: the INCLUDE-EXCLUDE (IN-EX) function, and the SORT function. The IN-EX function allows the user to specify a portion of the entire data set for output. The user may specify, for example, a state name, a collector, or a range of dates. By using a number of INCLUDE's or EXCLUDE's even more specific groups may be defined. An INCLUDE Ohio, EXCLUDE Franklin Co., INCLUDE Murphy, INCLUDE dates >1950, will produce a listing of all the entries for collections made by Murphy in Ohio, outside of Franklin Co., after 1950.

The SORT function enables the user to sort the data set or selected subset prior to output. The user supplies a control card indicating which fields should be sorted and in what order. A common choice would be first by taxon; then within taxon by collector; and finally within collector by number. The control card for this sort would be: TX CL CN.

Data Output

After manipulating the data, the TABLE and REPRESENTATIVE SPECIMEN functions cause the data set or selected subset to be listed. When using the TABLE function, the user furnishes a format card that directs REVISIO to list the requested information in columns. As an example, the format card, CL(10) DT(12) G1(15) G2(15) LC(30), will allot the first ten print positions to collector, the second 12 to the date, the next 15 to the major geographic division (probably country), the next 15 to the first subdivision (state), and the next 30 print positions to specific locality. Any of the eight pieces of information included in the entry may be requested and listed in this manner.

The REPRESENTATIVE SPECIMEN function causes the data set or subset to be listed in paragraph form with correct punctuation as used for lists of representative specimens in revisionary studies.

The END function brings REVISIO to normal termination.

Description of Procedures with REVISIO

Although different types of procedures can be accomplished either separately or in sequence with REVISIO, we believe one particular series of procedures to be most helpful for use in revisionary investigations (fig. 1). The following paragraphs describe briefly some of these steps.

We have found it very useful to generate checklists of data in varying formats as an aid to the revisionary studies in progress. REVISIO not only will generate data in representative specimen format but also in

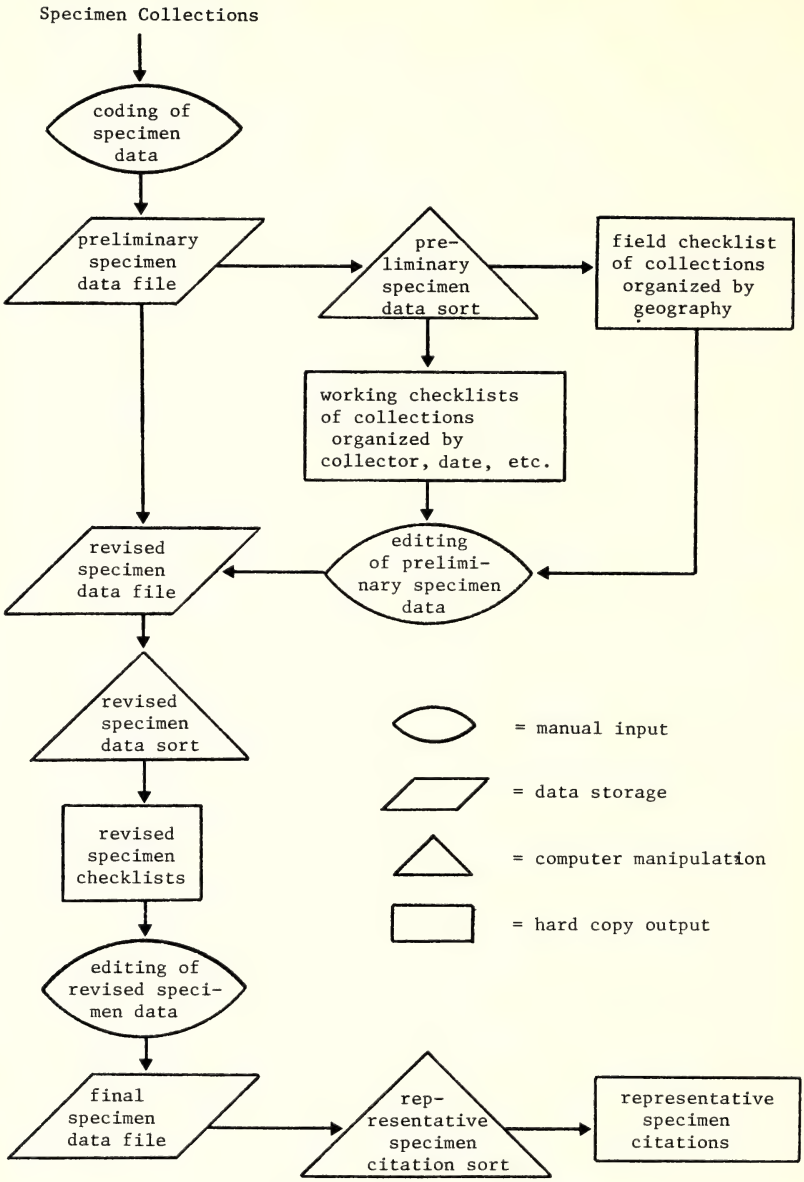

FIG. 1. Flow chart of procedures with REVISIO.

numerous other modes. For example, we have found it helpful to obtain a print-out of the specimen data that centers on the collector and his numbers, followed by the other information, for the following reasons: (1) locating type specimens in collections at hand; (2) detecting errors

in data, such as variant or erroneous spellings in collector's names; (3) locating duplicated collection numbers of the same collector; and (4) making editorial changes in the way data are cited, e.g., eliminating unnecessary locality data. We have also found a list of collections ordered geographically by region along a proposed itinerary very helpful in field studies.

After all collections have been obtained and data from these have been entered into the specimen data file, final representative specimen listings can then be generated. The representative specimen format in REVISIO is one that is commonly used by revisionary workers. The order of data in each citation is: geography, locality, date, collector, number, and herbaria. The sequence of citation is: (1) alphabetical by country and then by state and county; (2) alphabetical by the name of the collector(s); and (3) numerical in ascending order by the collection number. All the proper punctuation of periods, colons, semicolons, and commas are added automatically, and herbarium abbreviations are arranged alphabetically and enclosed with parentheses. The finished product (fig. 2) is indented in proper paragraph form and is printed out to fit on a page size 8½ inches wide. Use of cards for data submission results in all upper-case letters (as shown), whereas data input through a time-share terminal gives both upper and lower-case capability.

Use of REVISIO vs. Conventional Procedures

Interest on the part of practicing taxonomists to use REVISIO might depend upon knowing the costs of using the program in comparison with conventional manual card-file techniques. Three aspects need to be compared: time, money, and accuracy.

```
  REPRESENTATIVE SPECIMENS. EL SALVADOR. AHUACHAPAN:  NEAR
ATACO, 19 JAN 1947, STANDLEY & PADILLA V. 2633 (F).  SAN
SALVADOR:  SAN SALVADOR, JAN 1923, CALDERON 1456 (GH, NY).  SAN
VICENTE:  NEAR SAN VICENTE, 2-11 MAR 1922, STANDLEY 21653 (GH).
GUATEMALA. GUATEMALA:  NEAR FINCA LA AURORA, 1938-39, AGUILAR
1 (F);  VILLA CARLOTTA, 29 NOV 1896, SELER, C. & E. 2484 (GH,
NY).  JUTIAPA:  JUTIAPA, WITHOUT DATE, MORALES R. 1362 (F).
ZACAPA:  SIERRA DE LAS MINAS, TRAIL ABOVE RIO HONDO, 11 OCT 1939,
STEYERMARK 29549 (F).  MEXICO. GUERRERO:  7.2 MI S OF
CHILPANCINGO ON RTE 95, 11 SEP 1973, STUESSY & GARDNER 3146 (OS);
7.1 MI S OF PALO BLANCO ON RTE 95, 11 SEP 1973, STUESSY & GARDNER
3152 (OS).
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Fig. 2. Example of a representative specimen listing produced by REVISIO.

It is somewhat difficult to compare directly the time involved with REVISIO versus traditional methods. Inherent in the difficulty is the usual lack of familiarity of most taxonomists or herbarium secretaries with a keypunch machine, whereas these same people are usually skilled with a typewriter. To put the comparison on equal grounds, if the user is skilled to a high degree on both machines, in our experience, use of the keypunch for data input does take a little more time than with a typewriter. However, the subsequent direct computer listing of representative specimens is much faster than having to type them out by hand. In general, we can say that if small amounts of data are involved, say, fewer than 100 collections, and no additional lists or sorts are wanted—only the representative specimen listing—then it probably is faster to operate with conventional techniques. However, if more than 100 collections are involved, and/or if many data manipulations are desired, then use of REVISIO should result in a net saving of time. Obviously, the more data involved and the greater the number of manipulations desired, the more time will be saved by using the computer.

If one does not include time in cost analysis, then the use of REVISIO is more expensive than conventional methods. Computer cards are available gratis or at minimal cost ($2/thousand), and keypunch machines are accessible at no charge at many institutions. Although use of the keypunch and cards is minimal, use of computer time is expensive. A computer run for a representative specimen printout with REVISIO will vary in cost from about five to ten dollars (15–20 seconds CPU), depending upon the size of the data set being used.

If one is careful in the initial input of data with REVISIO, the accuracy of the sorted and printed information is astonishing. Once the data have been punched error-free on the cards, the computer will perform countless manipulations with no mistakes. This is a decided advantage in dealing with representative specimen data, because errors can so easily occur in each retyping step with conventional procedures. Another advantage in using REVISIO is the opportunity to edit data several times in differing formats before the final representative specimen list is produced. This procedure helps eliminate errors that were inadvertently made at time of original data input.

In summary, if small amounts of data (100 collections or less) are being processed, or if money for computer time is not available, then use of REVISIO is not recommended. However, because most revisionary studies involve several thousands of collections, many taxonomists may find the program helpful. Computer operation costs must be met, of course, but many institutions have mechanisms for allowing time to be obtained, if a genuine need is shown. Perhaps the best way for taxonomists to learn if REVISIO is suited for their own studies, is to try it at their home institutions. Copies of the program, sample data, and a user's manual are available from the second author.

Acknowledgments

The Instructional and Research Computer Center of Ohio State University provided computer time for the development of REVISIO. Certain aspects of this study were supported by National Science Foundation Grant GB-37678. Thanks go to Drs. T. J. Crovello and E. D. Rudolph for critical evaluation of the final manuscript.

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A STUDY OF SOME INTERMOUNTAIN VIOLETS (VIOLA SECT. CHAMAEMELANIUM)

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As a result of a cooperative study between Drs. Milo S. Baker and Jens Clausen, a classification for North American violets of sect. *Chamaemelanium* subsects. *Purpureae, Nuttallianae,* and *Chrysanthae* was proposed in a series of papers (Baker 1935, 1947, 1948, 1949a, 1949b, 1953, 1957, 1960; Clausen 1951, 1964b). This classification, as well as certain other cytotaxonomic, ecological, and evolutionary aspects of these violets, was reviewed by Clausen (1964a). In the review, Clausen expressed the need for an extensive cytological investigation of these violets in order to provide a firmer basis for their classification. This paper includes reports of new chromosome counts and observations of natural hybridization and morphology of some *Chamaemelanium* violets from the Intermountain Region and brief discussion of the taxonomic and evolutionary implications of this information.

METHODS

Field studies were carried out during spring and early summer of 1966, 1967, and 1969. Young flower buds were fixed in Newcomer's solution and chromosome numbers were determined from pollen mother cells using a standard aceto-carmine squash technique. In some cases it was possible to make chromosome counts from mitotic divisions in anther wall cells. Counts were documented with camera lucida drawings from fresh smears. Some slides were made permanent using the carbon dioxide quick-freeze method (Bowen, 1956). Pollen fertility was determined by staining pollen with methylene blue in lactophenol. Voucher specimens for all plants cited in this paper are deposited at UTC.

Herbarium specimens of relevant taxa were studied from the following herbaria: COLO, DS, ISC, JEPS, MO, MONT, RM, UC, US, UT, and UTC.

RESULTS AND DISCUSSION

Subsect. *Purpurea*

Clausen (1964a) placed three species in subsect. *Purpurea*: *Viola purpurea* Kell., $n=6$, with ten, mostly Californian, subspecies; *V. quercetorum* Baker & Clausen, $n=12$; and *V. utahensis* Baker & Clausen, $n=12$. Three of these taxa occur in the Intermountain Region: *V. purpurea* subsp. *atriplicifolia* (Greene) Baker & Clausen, *V. purpurea* subsp. *venosa* (Wats.) Baker & Clausen, and *V. utahensis*.

On the basis of their descriptions and herbarium sheet annotations, Baker and Clausen characterized *Viola purpurea* as a taxon variable in the shape of leaves and in the type of leaf margin. For the Intermountain Region small, purple-leaved plants with margins ranging from serrate to crenate were included under *V. purpurea* subsp. *venosa,* and under *V. purpurea* subsp. *atriplicifolia* were included all those small, purple-leaved forms whose leaf margins were deeply crenate to sublobate. Plants with green or purple leaves and a more or less regularly serrate leaf margin were placed under *V. utahensis.* Treated in this manner, subsp. *venosa* is quite intermediate between the other two taxa making it difficult to separate subsp. *venosa* from subsp. *atriplicifolia* at one extreme, while smaller plants of *V. utahensis* are almost impossible to distinguish from subsp. *venosa* at the other extreme.

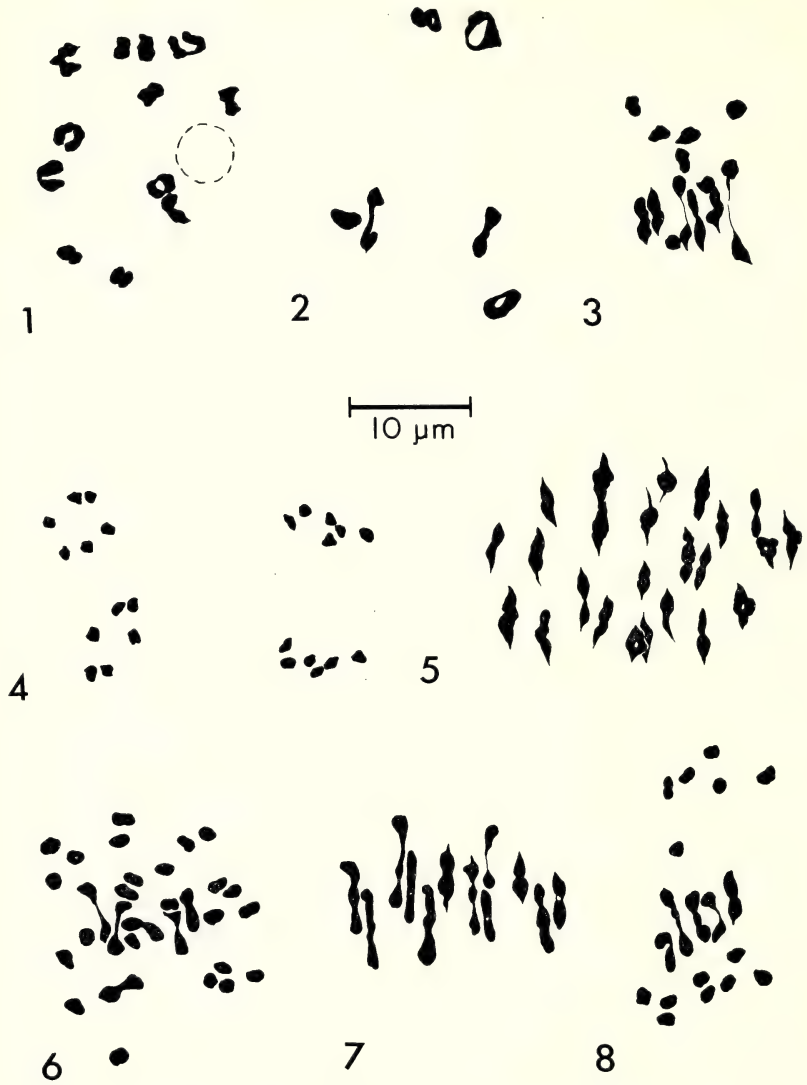
During chromosome number determinations it was discovered that plants with $n=12$ could be distinguished from those with $n=6$ on the basis of leaf margin. Tetraploid plants have serrate margins, whereas diploid plants have crenate margins. The tetraploid plants correspond to *V. utahensis* and the diploid plants correspond to *V. purpurea.* This correlation made it possible to distinguish between these two species with a high degree of confidence.

Meiosis in *Viola utahensis* was always regular with 12 bivalents at metaphase I (fig. 1), and pollen stainability was always well over 95 percent.

The size of plants of *Viola utahensis* is strongly correlated with elevation. Plants of low foothills and valleys are largest and mountain plants decrease in stature with increasing elevation. A distinctive series of green-leaved populations occurs in the Cache and Salt Lake Valleys of northern Utah, whereas mountain populations always have leaves with purple pigmentation. However, in several foothill areas extensive integradation occurs between these color forms, suggesting that they are of no taxonomic significance.

Viola utahensis is found primarily in open sagebrush areas from 1,200 to 2,150 m. In the southern part of its range in central Utah, it is often found growing under scrub oak, *Quercus gambelii* Nutt. Its range extends from Butte County, central Idaho, south to San Pete County, Utah, and from the East Humboldt Mountains, Elko County, Nevada, east to Lincoln County, Wyoming. This extends the range considerably from that delimited by Clausen (1964a).

As mentioned above, all small, crenate-leaved plants examined of *Viola purpurea* have $n=6$. Meiosis is regular and pollen stainability high (fig. 2). When all tetraploid, serrate-leaved plants are included under *V. utahensis,* there is no further basis for distinguishing subsp. *atriplicifolia* and *venosa,* so that subsp. *atriplicifolia* should be considered synonymous with subsp. *venosa.* Recognized in this sense, *V. purpurea* subsp. *venosa* occurs throughout the Intermountain Region, north into Washington, Idaho, Wyoming, and Montana, and south into



FIGS. 1–8. Camera lucida drawings of meiotic chromosomes of *Viola*. 1. *V. utahensis,* diakinesis, $n = 12$, *Davidse 1722A*. 2. *V. purpurea* subsp. *venosa,* late diakinesis, $n = 6$, *Davidse 1725*. 3. *V. purpurea* subsp. *venosa* × *V. utahensis,* metaphase I, $6_{II} + 6_{I}$, *Davidse 1722*. 4. *V. vallicola,* telophase II, $n = 6$, *Davidse 1720*. 5. *V. praemorsa* subsp. *major,* metaphase I, $n = 24$, *Davidse 1739*. 6. *V. praemorsa* subsp. *major* × *V. utahensis,* metaphase I, $6_{II} + 24_{I}$, *Davidse x-44C*. 7. *V. beckwithii,* metaphase I, $n = 12$, *Davidse x-5*. 8. *V. utahensis* × *V. beckwithii,* metaphase I, $5_{II} + 14_{I}$, *Davidse 1006*.

the higher mountains of Arizona. Altitudinally, it ranges from 1,800 to 3,050 m. It is associated with sagebrush or relatively open spaces in forested areas up to timberline.

Subsect. *Nuttallianae*

Clausen (1964a) recognized the following six species in subsect. *Nuttallianae*: *Viola vallicola* A. Nelson, $n=6$; *V. tomentosa* Baker & Clausen, $n=6$; *V. nuttallii* Pursh, $n=12$; *V. linguaefolia* Nutt., $n=18$; *V. bakeri* Greene, $n=24$; and *V. praemorsa* Dougl. ex Lindl. with three subspecies, $n=18$ and 24. This treatment is similar to that of Baker (1957), except that Baker considered *V. linguaefolia* to be a subspecies of *V. praemorsa* and he recognized one more subspecies of *V. praemorsa.* Three taxa, *V. vallicola, V. linguaefolia,* and *V. praemorsa* ssp. *major* (Hook.) Baker & Clausen occur within the Intermountain Region and were studied.

The chromosome number of *Viola vallicola,* $n=6$, was confirmed for a large number of populations (Table 1; fig. 4). This number had previously been based on a single determination. *Viola vallicola* has usually been considered to be closely related to the more eastern *V. nuttallii* and Russell (1965) considered the two species indistinguishable. However, from field observations and a comparison of a large number of herbarium specimens, it is clear that the diploid *V. vallicola* can be reliably separated from the tetraploid *V. nuttallii* on a morphological basis. *Viola vallicola* has cordate to truncate leaf bases, whereas *V. nuttallii* has cuneate leaf bases. *Viola vallicola* is very widely distributed from east of the Cascades and Sierra Nevada to the Great Plains just west of the Missouri River, and from the Canadian Plains south to Colorado. *Viola nuttallii* is found only east of the Continental Divide. It would be highly desirable to study the two species cytologically in their area of sympatry. Clausen (1964a) speculated that a diploid race of *V. nuttallii* may exist somewhere in this area, but there is no evidence for this.

Clausen (1964a) indicated that *Viola linguaefolia* was very similar morphologically to *V. praemorsa* subsp. *major* and he considered the difference in chromosome number to be the most reliable means of distinguishing the two taxa. *Viola linguaefolia* was reported to have $n=18$ on the basis of two counts, one from Latah County, Idaho, and another from Cache County, Utah (Baker, 1949b; Clausen, 1964a; Gershoy, 1934). Four counts of $n=24$ were reported for *V. praemorsa* subsp. *major* (Baker, 1949b; Clausen, 1964a). However, the hexaploid number for *V. linguaefolia,* $n=18$, could not be confirmed for plants from nine populations from Utah, Nevada, and Idaho, all within the range of *V. linguaefolia.* All plants had $n=24$ with regular meiosis and high pollen fertility (Table 1; fig. 5). For this reason and because no reliable morphological differences could be found, *V. linguaefolia* should be considered synonymous with *V. praemorsa* subsp. *major.*

TABLE 1. CHROMOSOME NUMBERS OF INTERMOUNTAIN VIOLA SPECIES. Collection numbers without name refer to Davidse collections.

V. beckwithii T. & G.; $2n = 12_{II}$.
IDAHO: Butte Co.: 2 mi NE of Butte Co. border along U.S. Hwys. 20 and 26, *1755*.
UTAH: Cache Co.: Millville, *1019;* 0.3 mi W of Wellsville, *x-4, x-5, 286*.

V. beckwithii × *V. utahensis;* $2n = 6_{II}+12_{I}$.
UTAH: Cache Co.: 0.3 mi W of Wellsville, *x-6, 1002, 1003, 1004, 1005, 1006*.

V. praemorsa Dougl. ex Lindl. subsp. *major* (Hook.) Baker & Clausen; $2n = 24_{II}$.
IDAHO: Bear Lake Co.: 8 mi W of Ovid, *1046*. Franklin Co.: 20.5 mi W of Ovid, *x-39, 1033*. Owyhee Co.: Silver City Range, *1746*.
NEVADA: Elko Co.: 10 mi NW of jct. Nev. Hwy. 51 and Nev. Hwy. 11, *1738, 1739;* Chicken Creek Summit between Jack Creek and Deep Creek, *1742;* Columbia Creek along road between Deep Creek and Mountain City, *1744*. Humboldt Co.: Lye Creek, Santa Rosa Range, *Gentry & Davidse 1640*.
UTAH: Cache Co.: mouth of Wellsville Canyon *x-22, x-24, 1015;* 20.5 mi up Logan Canyon, *1041*.

V. praemorsa subsp. *major* × *V. utahensis;* $2n = 6_{II} + 24_{I}$.
IDAHO: Bear Lake Co.: 8 mi W of Ovid, *x-44C*.

V. purpurea Kell. subsp. *venosa* (Wats.) Baker & Clausen; $2n = 6_{II}$.
IDAHO: Bear Lake Co.: 8 mi W of Ovid, *x-44B, x-45, 1047A*. Camas Co.: Silver City Range, *1748*.
NEVADA: Elko Co.: Chicken Creek Summit between Jack Creek and Deep Creek *1740, 1741;* Pequop Summit along U.S. Hwy. 40, Pequop Mts., *1731;* 9 mi S of Wells, *1735;* 10 mi NW of jct. Nev. Hwy. 51 and Nev. Hwy. 11, *1737*. Humboldt Co.: 14 mi N of Winnemucca, *Gentry & Davidse 1553*.
UTAH: Cache Co.: 31 mi NE of Logan, Logan Canyon, *1724, 1725*. Rich Co.: 4 mi W of Garden City, *382, 1721;* 2 mi W of Garden City, *1038*.

V. purpurea subsp. *venosa* × *V. utahensis;* $2n = 6_{II} + 6_{I}$.
IDAHO: Bear Lake Co.: 8 mi W of Ovid, *1047B*.
NEVADA: Elko Co.: 9 mi S of Wells, *1734*.
UTAH: Cache Co.: 31 mi NE of Logan, Logan Canyon, *1723A*. Rich Co.: 4 mi W of Garden City, *1722A*.

V. utahensis Baker & Clausen; $2n = 12_{II}$.
IDAHO: Bannock Co.: 5 mi E of Inkom, *1759*. Bear Lake Co.: 8 mi W of Ovid, *x-44D*. Butte Co.: Big Southern Butte, *1756*. Franklin Co.: 18.8 mi W of Ovid, *1035;* 20.5 mi W of Ovid, *x-43, 1034;* just N of Franklin Cemetery, *x-29, x-31, x-36, x-37*.
NEVADA: Elko Co.: 9 mi S of Wells, *1733*.
UTAH: Box Elder Co.: 0.5 mi E of Deweyville, *x-18, x-19, 992;* 1 mi SE of Honeyville, *x-21, 308, 994, 995, 996*. Cache Co.: 14 mi up Logan Canyon *302*; 20.5 mi up Logan Canyon, *1042*; 30 mi up Logan Canyon, *1723;* 0.5 mi W of Mendon, *x-13, x-17*; Richmond, *1030*; mouth of Wellsville Canyon, *1017*; 0.3 mi W of Wellsville, *x-1, x-2, 1051*; 1.5 mi NW of Wellsville, *x-7, x-8*. Rich Co.: 4 mi W of Garden City, *1722*; 1 mi W of Garden City, *1044*. Salt Lake Co.: between Mt. Olympus and Big Cottonwood Canyon, *1713, 1716;* 3 mi up Lamb's Canyon, *1760*. Utah Co.: 4 mi NW of Alpine, *1719*.

V. vallicola A. Nelson; $2n = 6_{II}$.
IDAHO: Bear Lake Co.: 1.3 mi W of Ovid, *x-38, x-40, x-41, x-42A*. Blaine Co.: 3 mi W of Carey, *1754*. Camas Co.: 12 mi E of Fairfield, *1753*. Franklin Co.: just N of Franklin Cemetery *x-30, x-32, x-34, x-35*. Owyhee Co.: 13 mi NE of Riddle, *1745*.

TABLE 1. *Continued.*

NEVADA: Elko Co.: Pequop Summit along U.S. Hwy. 40, Pequop Mts. *1731*; 2 mi S of Wells, *1732*; 10 mi NW of jct. Nev. Hwy. 51 and Nev. Hwy. 11, *1736*. Humboldt Co.: Lye Creek, Santa Rosa Range, *Gentry & Davidse 1639*.

UTAH: Box Elder Co.: 0.5 mi E of Deweyville, *x-20, 993*; S end of Howell Valley, *Davidse & Hatch 1009*; 2 mi S of Stanrod, *Davidse & Hatch 1011*. Cache Co.: Spring Hollow, Logan Canyon, *282*; 20.5 mi up Logan Canyon, *1040*; 0.5 mi W of Mendon, *x-14, x-15*; mouth of Wellsville Canyon, *x-27, x-28*; 0.3 mi W of Wellsville, *1053*. Rich Co.: 2 mi W of Garden City, *1037*. Utah Co.: 0.5 mi NE of Alpine, *1720*.

The previous count of $n=18$ for *V. linguaefolia* from Utah may well have been based on a hybrid between *V. praemorsa* subsp. *major* and *V. utahensis,* similar to the one reported below in the section on hybridization. The count for *V. linguaefolia* from Latah County, Idaho, may represent an inland extension of the typically coastal hexaploid (Clausen, 1964a) *V. praemorsa* subsp. *praemorsa* along the Columbia-Snake River drainage system.

Subsect. *Chrysanthae*

In subsect. *Chrysanthae*, characterized by rosettes of deeply dissected leaves, Clausen (1964a) recognized five species: *Viola sheltonii* Torr., $n=6$; *V. douglasii* Steud., $n=12$ and 24; *V. hallii* Gray, $n=36$; *V. trinervata* Howell, $n=12$ (Carr, 1969); and *V. beckwithii* T. & G. *Viola bonnevillensis* was described from Utah by Cottam (1939). This name was not discussed by Baker and Clausen but was treated as a synonym of *V. beckwithii* by Holmgren and Reveal (1966). *Viola beckwithii* and plants corresponding to *V. bonnevillensis* (see below under hybridization) have been studied.

Chromosome counts from three populations in Utah and Idaho show that *Viola beckwithii* is a tetraploid, $n=12$, with regular meiosis (Table 1; fig. 7). This is the first count for this species.

Hybridization

Viola purpurea subsp. *venosa* × *V. utahensis*.—In Cache County, Utah, Elko County, Nevada, and Bear Lake County, Idaho, hybridization between *V. utahensis* and *V. purpurea* subsp. *venosa* has been observed. In the Utah and Idaho localities the parent species grew in mixed populations, but in Nevada, *V. purpurea* subsp. *venosa* grew on the west slope of a ridge while *V. utahensis* occupied the drier east slope. The hybrid was found on the summit of the ridge where the two species overlapped.

Morphologically the hybrids appear almost identical with *V. utahensis*. In the field they can best be recognized by their vigorous growth compared to surrounding plants. However, definitive confirmation of their hybrid nature can be obtained only from chromosome or pollen

stainability studies. Hybridization is apparently limited to the areas where the parent species occur in mixed stands. Frequency of hybridization is difficult to judge, but it is probably not high. The hybrids were triploid with usually $6_{II}+6_{I}$ at metaphase I, although in occasional PMC's configurations of $5_{II}+8_{I}$ or $4_{II}+10_{I}$ were observed (fig. 3). Pollen stainability varied from 0–29 percent. Unequal distribution of chromosomes at anaphase I and lagging univalents were frequent irregularities. Stainable pollen was probably not all fertile since some of the grains were not as well filled with starch and cytoplasm as those of non-hybrid plants. Pollen grains also differed widely in size. This results from abnormal pollen formation caused by meiotic irregularities. In those instances where lagging univalents do not become incorporated into the four newly formed nuclei at telophase II, ensuing cytokinesis forms cell walls around micronuclei creating chromosomally deficient microspores. The size of these microspores is probably correlated with the number of chromosomes that are included in the micronuclei. This phenomenon, termed polyspory, has previously been reported in widely different groups of *Viola* (Bamford and Gershoy, 1930; Manch, 1937; Pettet, 1964; Schmidt, 1961). In rare instances, the unpaired chromosomes may be totally excluded from one of the daughter cells after the first division. In such a case there is a potential for the formation of two fertile pollen grains and this mechanism may account for the low percent of apparently normal pollen that is observed in the hybrids.

Baker and Clausen (Baker, 1949a) have suggested that *V. utahensis* is an allopolyploid derivative of hybrids between *V. purpurea* subsp. *venosa* and *V. vallicola*. If this were true, the hybrid between *V. purpurea* subsp. *venosa* and *V. utahensis* should have a $6_{II}+6_{I}$ configuration at metaphase I. This was the maximum pairing observed in the hybrids and, therefore, tends to confirm Baker's hypothesis. Unfortunately, the second unpaired genome of the hybrid cannot be positively identified as the *vallicola* genome on the basis of these few natural hybrids. *Viola vallicola* is the logical choice, however, since this is the only diploid plant now known that occurs in the same area with *V. purpurea* subsp. *venosa* and *V. utahensis*. Moreover, morphologically *V. vallicola* appears to be the only diploid species that could have been a parent.

Although on the basis of leaf morphology alone, *V. utahensis* and *V. purpurea* subsp. *venosa* would, perhaps, not be considered distinct at the species level, the barrier to gene exchange through sterile, or nearly sterile, triploids indicates that these two taxa are best maintained as closely related, but distinct, species.

Viola praemorsa subsp. *major* × *V. utahensis*.—One plant similar to *V. praemorsa* subsp. *major*, but with purple coloration of the leaves, was discovered to have the hexaploid number $n=18$. Unfortunately only a few PMC's were suitable for chromosome counts and meiotic interpretation. These showed a configuration of $6_{II}+24_{I}$ at late metaphase I (fig. 6). Stainable pollen was only 58 percent. The single plant was

found in Bear Lake County, Idaho, in the same mixed population of *V. purpurea* subsp. *venosa* ($n=6$), *V. utahensis* ($n=12$), and *V. praemorsa* subsp. *major* ($n=24$) where a *V. purpurea* subsp. *venosa* × *V. utahensis* hybrid was discovered. The chromosome number of each of the parent species from this population was reconfirmed and all had normal stainable pollen. The intermediate chromosome number, irregular meiosis, and lowered pollen fertility of the single hexaploid plant in a population of normal parent plants leaves little doubt that the hexaploid was a hybrid between *V. praemorsa* subsp. *major* and *V. utahensis*. It may have been on a similar plant that the previous record of $n=18$ for *V. linguaefolia* (=*V. praemorsa* subsp. *major*) from Utah was based, since both plants of *V. praemorsa* subsp. *major*, $n=24$, and *V. utahensis*, $n=12$, occur in the locality.

Clausen (1964a) stated that *V. vallicola* might have been one of the parents of *V. linguaefolia* (=*V. praemorsa* subsp. *major*). If this were indeed true, then the paired genome observed in the hybrid probably corresponds to a commonly shared *vallicola* genome in *V. utahensis* and *V. praemorsa* subsp. *major*. However, only controlled hybridization can confirm this speculation.

Viola beckwithii × *V. utahensis*.—Plants corresponding to the type of *V. bonnevillensis* were found growing in a large mixed population of *V. beckwithii* and *V. utahensis* near Wellsville, Utah. Another single plant of *V. bonnevillensis* was found near Providence, Cache County, Utah. Cottam (1939), when describing *V. bonnevillensis*, mentioned the possibility that this species was a hybrid between *V. beckwithii* and *V. purpurea* subsp. *venosa* (= *V. utahensis* of this treatment). This seems indeed to be the case. Morphologically the hybrids are intermediate in leaf shape and flower color. The leaves of *V. utahensis* are entire and those of *V. beckwithii* are palmatisect with many lobes, while those of *V. bonnevillensis* are palmatifid with few lobes. Flowers of *V. utahensis* are deep yellow on the face and brown on the back, especially on the upper two petals. *Viola beckwithii*, in this population, had very dark violet upper petals, white lateral and spur petals, and a deep yellow center. The hybrid had purplish brown upper petals, very light yellow lateral and spur petals, and a yellow center. The lower petals also had variable amounts of brown pigments.

Seed was not set during the 1966 to 1968 growing seasons either in garden transplants or in plants growing in the field. Stigmas of the hybrids were artificially pollinated with *V. beckwithii* and *V. utahensis* pollen, but no seed was produced in either case, although the ovaries markedly increased in size for about a week.

The chromosome number of the hybrid was $n=12$, but meiosis was highly irregular. Up to 6 bivalents were observed at metaphase I, although the number was usually lower (fig. 8). Pollen stainability was only 9 percent and fertility may well be lower. Polyspory was also very frequent. Although homology of one genome of *V. beckwithii* and *V.*

utahensis may be indicated by the pairing, it is probably not a very close homology. Chromosomal bridges were often observed, indicating that the chromosomes of these genomes differed in a number of rearranged segments. The incomplete homology may indicate that an originally similar genome has had time to differentiate through gross chromosomal rearrangements in each of the parent species. The origin of these presumably partially homologous genomes cannot be identified at the present time but may be hypothesized to represent the genome of an ancestral diploid species that eventually gave rise to the several subsections of *Chamaemelanium* violets in the western United States.

A parallel to the Utah hybrid has been described from California where *V. quercetorum* and *V. douglasii* hybridize to produce offspring morphologically similar to the Utah hybrids and also having a $6_{II}+12_{I}$ chromosome configuration. Clausen (1964a) did not speculate on the origin of the paired genome but hypothesized that autosyndesis may have been involved.

Nondiscriminate insect pollinators, especially bee flies, syrphids, and flower flies, are no doubt largely responsible for interspecific hybridization among these *Viola* species. An interesting example of contrasting pollinator behavior was observed in the mixed *V. beckwithii-V. utahensis* population near Wellsville, Utah. This population also contained the hybrid between these two species. Two species of bees were important pollinators in this population. The honey bee, *Apis mellifera* L., was species specific, i.e., individual bees visited either *V. utahensis* or *V. beckwithii* flowers, but not both. In contrast, individuals of *Anthophora ursina* Cresson visited both violet species indiscriminately, thus creating the opportunity for hybridization through cross pollination. In other populations flies of the genera *Eristalis* and *Bombylius* have been frequently observed to visit the yellow flowered species *V. vallicola, V. utahensis,* and *V. praemorsa* subsp. *major* indiscriminately and insects such as these probably play a major part in the interspecific pollination that leads to occasional hybridization among these species.

Acknowledgments

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TAXONOMY OF MENTZELIA MOLLIS AND ALLIED SPECIES (LOASACEAE)

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Mentzelia mollis Peck is a small annual endemic to the Succor Creek region in the Owyhee Desert of southeastern Oregon and southwestern Idaho. During a taxonomic and ecological study designed to clarify the relationship of *M. mollis* to other members of the genus, two poorly understood taxa came under investigation (Glad, 1975). One had been found in Leslie Gulch, a few kilometers west of Succor Creek, by Patricia L. Packard; the other had been noted in Colorado and Utah by Henry J. Thompson, who tentatively identified it as *M. mollis*. This paper reports conclusions reached concerning taxonomy of the three taxa.

Within *Mentzelia* sect. *Trachyphytum* T. & G., taxonomic interpretations are often difficult, because differences in morphology from one

species to another are subtle. There are at least two polyploid complexes, the *Mentzelia affinis* Greene complex and the *Mentzelia albicaulis* (Hook.) T. & G. complex; each has species that show wide morphological variations among their populations. However, these polyploid complexes can be separated from each other on the basis of seed morphology. It has long been noted that seed shape, marking, and surface texture are dependable taxonomic characters (Darlington, 1934), and recent workers have emphasized seed morphology as a basis for separating species (Thompson and Roberts, 1974). Other characters that are used to distinguish species are petal, bract, and leaf shape, petal color, and capsule shape and orientation (Zavortink, 1966). In the present study, reliance has been placed on these morphological features, since it has not been feasible to apply the ultimate species criterion of genetic compatibility via hybridization experiments (cf. Thompson and Roberts, 1971). Ecological data for *M. mollis* and its allied taxa proved to be of additional interest, however. Herbarium records by earlier collectors rather consistently refer to the occurrence of *M. mollis* on grey or green clay soil. This suggestion of an edaphic restriction was confirmed for all populations studied, and this factor, together with geographical isolation, appears to contribute to the variation pattern and endemism of these species.

Ecological Observations

Both *M. mollis* and the Leslie Gulch *Mentzelia* are found only on green or grey montmorillonite derived from the Sucker Creek formation, a tuffaceous sedimentary rock (Baldwin, 1964). In all instances both taxa were members of depauperate plant communities that did not include the common shrubs (*Atriplex* and *Artemisia* spp.) and grass (*Bromus tectorum* L.) that are ubiquitous in the Owyhee Desert. *Mentzelia mollis* consistently is associated with the same three species: *Cleomella macbrideana* Pays., *Phacelia lutea* (H. & A.) J. T. Howell, and *Monolepis pusilla* Torr. In no instance was the population of *M. mollis* contiguous with the *Artemisia-Bromus* community. The Leslie Gulch *Mentzelia* was found at the base of talus slopes that supported only scattered *Artemisia* and very sparse grasses and forbs. Soil samples were taken at a population of *M. mollis* near Rockville, Oregon, and from one site in Leslie Gulch. The former showed 1,360 ppm of potassium, the latter 6,400 ppm, both extraordinarily high concentrations. Although alkaline soil is common in this area of low rainfall, the potassium content of the soil that supports these populations could well account for both the exclusion of the normal *Artemisia*-dominated vegetation and the apparent edaphic endemism of the Mentzelias.

No data are available concerning plant associates of the Colorado-Utah *Mentzelia*. Information from specimens examined indicates that it, too, shows soil specificity, with Mancos shales, grey clay, and gumbo having been noted as substrates.

Morphological Comparisons

Despite their apparent similarity in floral morphology and soil specificity, *M. mollis* and the Leslie Gulch *Mentzelia* show rather marked morphological differences. *Mentzelia mollis* is relatively stout and many-branched, having ovate-lanceolate leaves with entire margins, sparse pubescence, obovate and mucronate petals, a style that is longer than the stamens, and very small, irregularly angled or rounded seeds that are minutely and finely papillose. It is tetraploid, $2n = 36$ (Ore., Malheur Co., *Glad 74–65,* OCS, and *Packard 74–37,* CIC). The Leslie Gulch *Mentzelia,* on the other hand, is only sparsely branched, has linear to ovate-lanceolate leaves, often with narrow, shallow lobes, dense pubescence, obovate to round petals, a style that is equal to or shorter than the stamens, and rather large irregularly angled to somewhat prismatic seeds with large, truncate papillae. It is octoploid, $2n = 72$ (type collection, see below).

The Colorado-Utah *Mentzelia,* seen only as herbarium specimens, is remarkably similar to *M. mollis,* differing primarily in floral size and morphology. The seeds are larger, with easily observed pointed papillae.

Both Oregon taxa show considerable vegetative and floral variation among populations and among individuals maturing at different times in the season; the most dependable taxonomic character to distinguish between them is seed morphology. A scanning electron microscope was used to photograph seeds of these two taxa, as well as of the Colorado and Utah specimens that closely resemble *M. mollis* in all but floral morphology. Three other species of sect. *Trachyphytum* (*Mentzelia dispersa* S. Wats., *M. albicaulis,* and *M. affinis*) were also examined.

The resulting comparisons (figs. 1 and 2) show certain distinctive differences in seed morphology. Both *M. affinis* (fig. 1, A and B) and *M. dispersa* (fig. 1, C and D) have obviously prismatic seeds, grooved on the angles. This is, in fact, the basis of separation of these two species from other members of sect. *Trachyphytum* (Thompson and Roberts, 1974). The papillae are low, truncate columns, closely set and relatively small as compared to those of other species in the section. Though nearly all other species have occasional seeds that are somewhat triangular in cross section, it is only in these two species that this characteristic is constant. *Mentzelia albicaulis* seeds (fig. 1, E and F) show the most marked differences from those of the preceding two species. They are often sharply, though irregularly, angled, never prismatic, and the papillae are high, pointed, and large in relation to seed size.

Of the three taxa under discussion, seeds of the Colorado and Utah *Mentzelia* (fig. 2, A and B) most closely resemble those of *M. albicaulis* in being irregularly angled and having high, pointed papillae. The Leslie Gulch specimen (fig. 2, C and D) has large but low truncate papillae whose flat tops have a textured concavity. While occasionally somewhat prismatic and grooved on the angles, they are more often irregularly angled or rounded. They are also among the largest seeds found in this

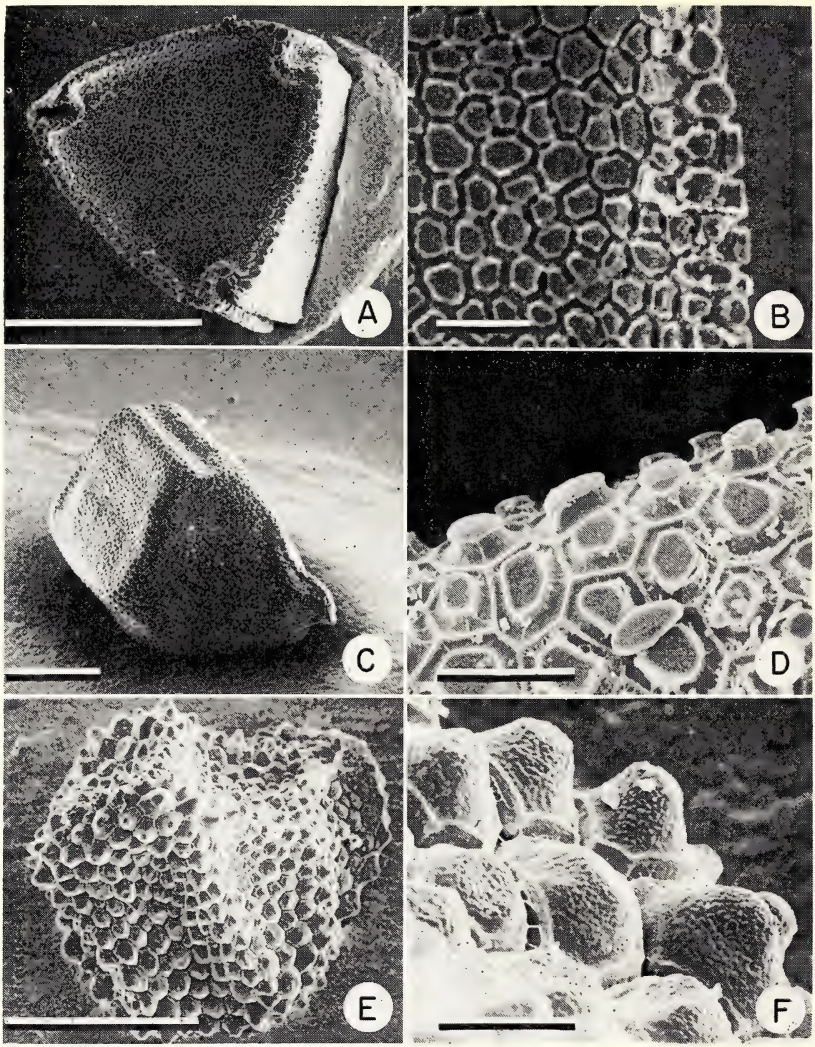

FIG. 1. Scanning electronmicrographs of seeds of *Mentzelia* spp. A and B, *M. affinis* (Calif., Kern Co., *Thompson 1557,* LA); C and D, *M. dispersa* (Ore., Harney Co., *Cronquist 8610,* LA); E and F, *M. albicaulis* (Ore., Harney Co., *Brown and Conrad EC042,* OSC). Scales: A, C, and E = 0.5mm; B, D, and F = 0.05mm.

group of species. At low magnification, seeds of *M. mollis* (fig. 2, E and F) appear to be quite smooth. Their shape is similar to that of other species in this group, but they are usually more rounded than seeds of either *M. albicaulis* or the *Mentzelia* from Colorado and Utah. Even at a magnification of 700×, the papillae are very small, low, and rounded, showing, incidentally, that the specific epithet may be applied to seed surface as well as to leaf pubescence.

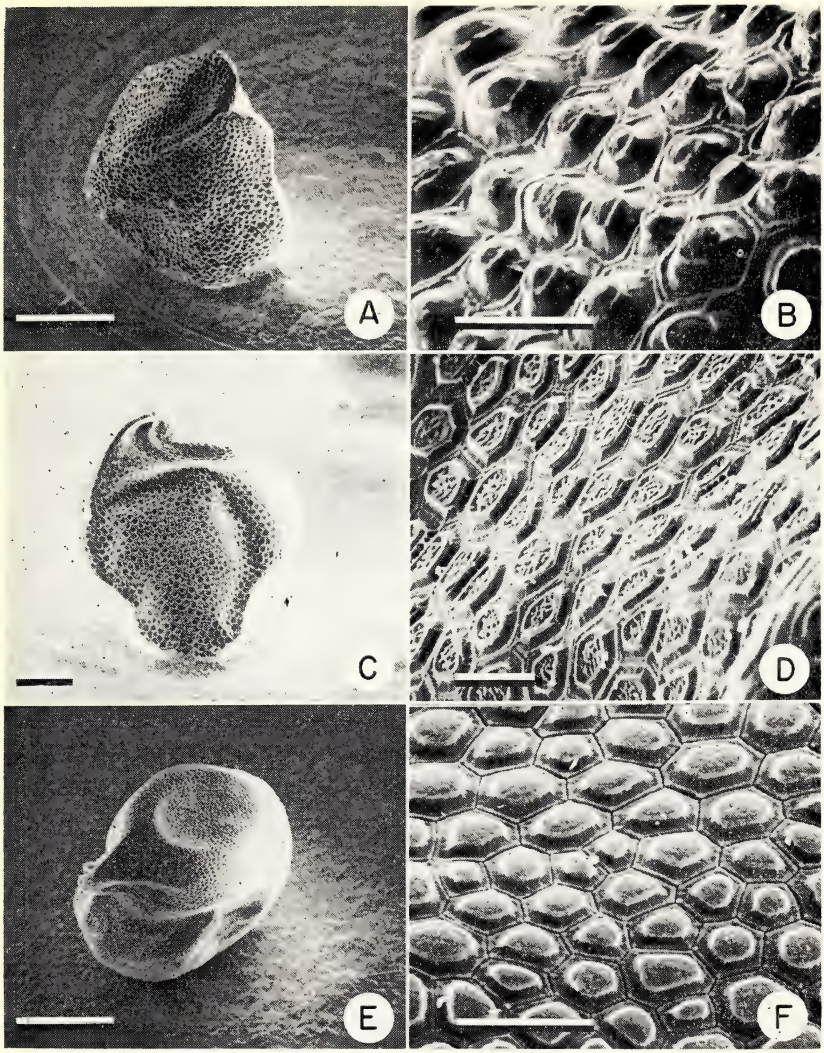

FIG. 2. Scanning electronmicrographs of seeds of *Mentzelia* spp. A and B, *M. thompsonii* (Colo., Montezuma Co., *Thompson 3540,* OSC) ; C and D, *M. parkardiae* (Ore., Malheur Co., *Glad 74–134,* OSC) ; E and F, *M. mollis* (Ore., Malheur Co., *Glad 74–116,* OSC). Scales: A, C, and E = 0.5mm; B, D, and F = 0.05mm.

TAXONOMIC CONCLUSIONS

Mentzelia mollis and the plants occurring in Leslie Gulch appear to represent two specifically distinct taxa, although they are only slightly separated geographically (fig. 3) and have superficially similar edaphic adaptations. Consistent and significant differences are seen in their chromosome numbers, as well as their vegetative, floral, and seed morphology. The chromosome difference might well act as a barrier to

successful interbreeding should any of the populations become sympatric. The *Mentzelia* from Colorado and Utah is disjunct geographically from the above two, and its range is not so localized (fig. 4). Although similar to *M. mollis* in habit and leaf shape, it has smaller petals that are obovate and retuse, and its seeds are distinctly papillose. It is proposed that these populations, too, be designated as a separate species. Future field studies of this plant, including chromosome counts and habitat descriptions, should tell more about its relationship to the taxa from the Succor Creek region.

Partial Key to Mentzelia sect. Trachyphytum
(modified from Thompson and Roberts, 1974)

1. Seeds angular or prismatic, regularly grooved along the three angles, surface appearing smooth at low magnification: . . . . . *M. affinis* complex
1. Seeds irregularly angled or rounded, not regularly grooved on the angles, surface generally appearing papillose at low magnification: *M. albicaulis* complex . . 2

2. Bracts lobed 3
2. Bracts entire 4

3. Bracts without white area at base . . *M. albicaulis* (in part)
3. Bracts with white area at the base . . *M. gracilenta* and allies

4. At least the oldest capsules recurved more than 90° *M. desertorum* and allies
4. None of the capsules recurved more than 90° 5

5. Rosette absent or loosely formed, basal leaves entire to scarcely lobed, upper leaves entire 6
5. Rosette present; basal leaves entire or with short or long irregularly toothed lobes 8

6. Leaves linear to linear-lanceolate, the lower sometimes with a few shallow lobes; branching sparse; seeds with low, truncate, microscopically reticulated papillae . *M. packardiae*
6. Leaves lanceolate to oblanceolate, entire; branching profuse; seeds with pointed or smoothly rounded papillae . . 7

7. Petals 6–15 mm, the apex mucronate; seed surface almost smooth, the papillae small, low, and slightly rounded . . . . . *M. mollis*
7. Petals less than 6 mm, the apex retuse; seed surface with high pointed papillae . . . . . *M. thompsonii*

8. Upper leaves broad-based, somewhat clasping; petals obovate or broadly ovate . . . . . *M. mojavensis*
8. Upper leaves not clasping, often entire; petals ovate *M. albicaulis* (in part)

Mentzelia packardiae Glad, sp. nov. Herba annua erecta 1–4 dm alta, caule parce ramoso crasso argento vel viridulo. Folia rosulae linearia integra aut lobata lobis angustis brevibus, caulis sessilia varie lineari aut ovato-lanceolata integra. Flores axillares solitarii nudi necnon in fasciculis terminalibus bracteis subtendi, bracteis sessilibus oblanceolatis integris amplectentibus. Sepala triangularia. Petala 5, 8–15 mm longa, lutea emaculata vel basi macula crocea, obovata vel rotunda, mucronata vel leviter retusa. Stamina 15–30. Stylus 4–10 mm longus, staminibus aequatus vel brevior. Capsulae axillares erectae cylindricae basi contractae 15–30 mm longae. Semina irregulariter angulata vel aliquantum prismatica brunneola interdum maculis atrobrunneis papillis numerosis humilibus truncatis.

TYPE: Oregon, Malheur County, Leslie Gulch 3.2 km southeast of Owyhee Reservoir, in green rock derived from the Sucker Creek Formation at base of talus slope, T25S, R44E, 26 June 1974, *Glad 74–76,* (Holotype: OSC!; isotypes: CIC!, NY!, LA!).

Plant annual, erect, 1–4 dm tall, sparsely branched, stems rather stout, white to pale green; basal leaves linear, entire, or with shallow narrow lobes; upper leaves linear to ovate-lanceolate, entire, sessile, and occasionally somewhat clasping; flowers solitary in the stem axils, and in terminal clusters subtended by bracts; bracts sessile, oblanceolate, entire, and somewhat clasping; sepals 5, triangular, about one-third as broad as long, recurved and persistent on the mature capsule; petals 5, 8–15 mm long, yellow, with or without an orange spot at the base, ovate to round, mucronate or slightly retuse; stamens 15–30, 4–10 mm long; style 4–10 mm long, equal to or shorter than the stamens; capsules erect, cylindrical, tapering slightly toward the base, the axillary capsules 15–30 mm long, the terminal capsules 8–25 mm long; seeds 10–20 per capsule, irregularly angled to slightly prismatic, sometimes with shallow grooves on the angles, brownish and sometimes with darker brown spots, 2.0 mm long and 1.5 mm wide, the surface with low, truncate papillae; chromosome number $2n=72$.

DISTRIBUTION (fig. 3): In rocky soil of high montmorillonite content at base of talus slopes along canyon walls, Leslie Gulch and its side canyons, Malheur County, Oregon, only.

Mentzelia thompsonii Glad, sp. nov. Herba annua erecta, 1–2 dm alta, ramosa caulibus confertis pallidis. Folia sessilia ovato-lanceolata integra. Flores axillares solitarii nudi necnon in fascicularis terminalibus bracteis subtendi, bracteis sessilibus oblanceolatis integris amplectentibus. Sepala triangularia. Petala 5, 1.5–4.0 mm longa, lutea obovata apice retusa. Stylus 1.5–3.0 mm longus, staminibus aequatus vel brevior. Capsulae axillares erectae cylindricae, 12–20 mm longae. Semina irregulariter angulata papillis numerosis acutis vel truncatis.

TYPE: Colorado, Montrose County, gypsum hills 7 miles east of Montrose, 6,000 feet, 30 May 1952, *W. A. Weber 7470* (Holotype: COLO!; isotypes: RSA!, WTU!, WS!).

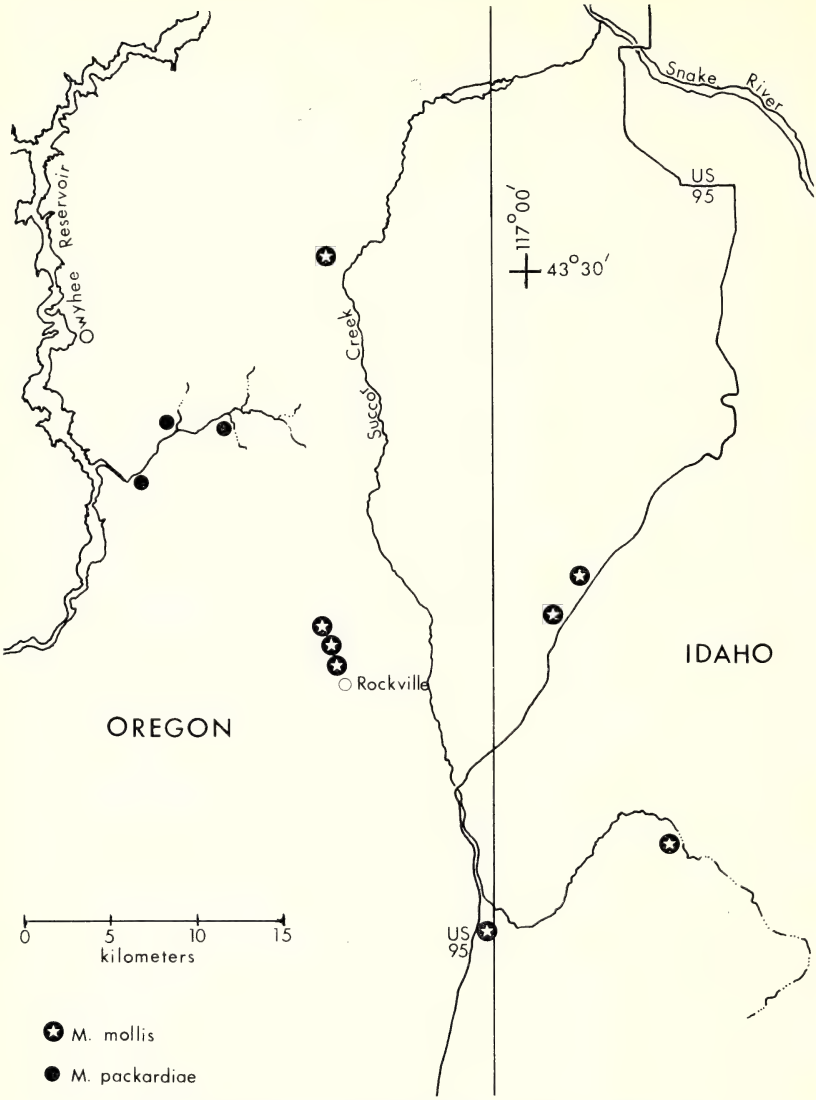

FIG. 3. Distribution of *Mentzelia mollis* and *M. parkardiae*.

Plant annual, erect 1–2 dm tall, moderately branched and compact, the stems pale; leaves ovate-lanceolate, entire, sessile; flowers solitary in the stem axils and terminal, subtended by bracts; bracts oblanceolate, green, entire and somewhat clasping; sepals 5, triangular; petals 5, 1.5–4.0 mm long, yellow, obovate, the apex retuse; style 1.5–3.0 mm long, equal to or shorter than the stamens; capsules erect, cylindrical, narrowing slightly at the base, the axillary capsules 12–20 mm long, the

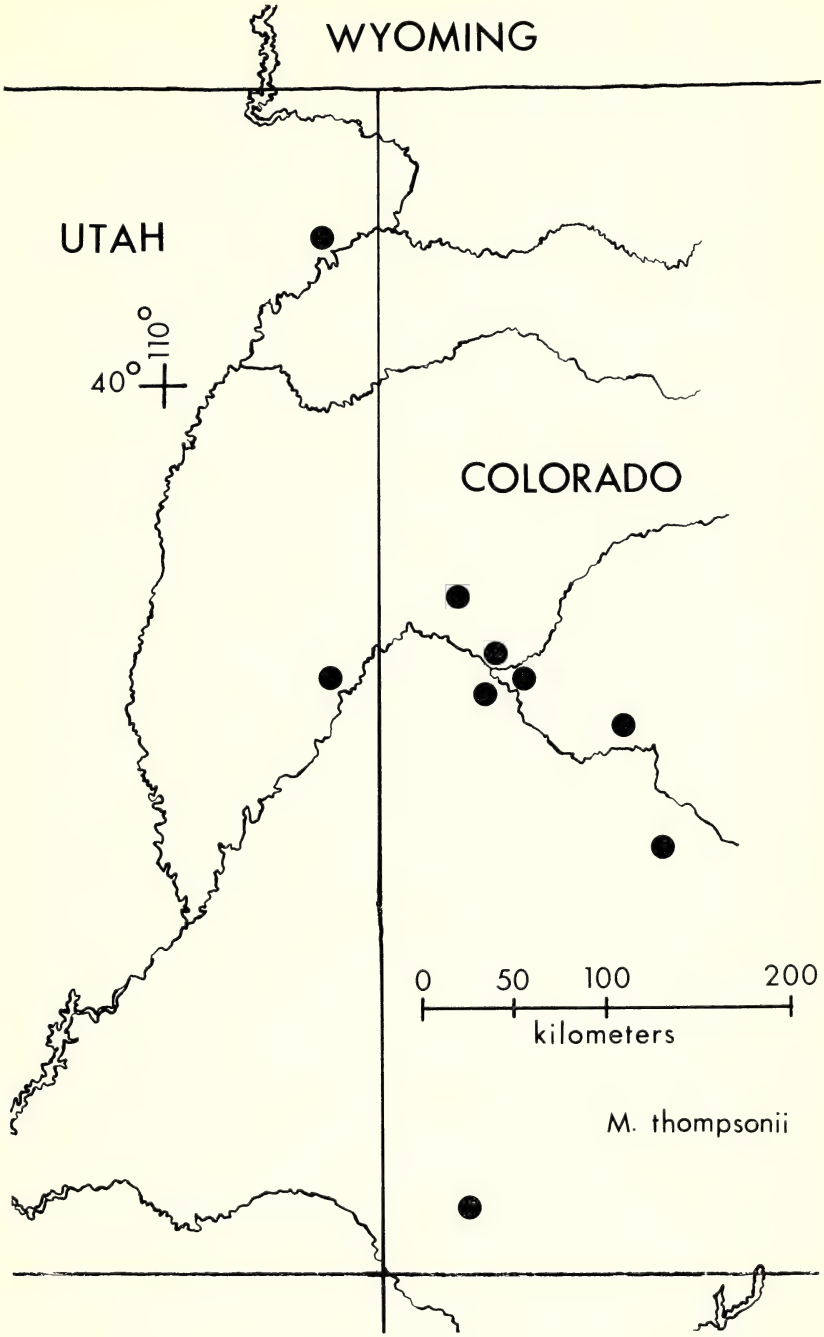

FIG. 4. Distribution of *Mentzelia thompsonii*.

terminal capsules 5–15 mm long; seeds 10–25 per capsule, irregularly angled, 1.2 mm long by 0.8 mm wide, the surface with small pointed to truncate papillae.

DISTRIBUTION (fig. 4): On grey clay of high desert hills along the Utah-Colorado border, 1200 to 1800 m.

Flowering time for both species is mid-May to late June. *Mentzelia thompsonii* has been identified both as *M. mollis* and *M. dispersa* in the past, but it is morphologically very different from both.

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A NEW SPECIES OF CHOLLA (CACTACEAE: OPUNTIA) FROM COAHUILA, MÉXICO

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A floristic study of the Bolsón of Cuatro Ciénegas and surrounding mountains, Coahuila, México, has revealed a new species of cholla (Cactaceae: *Opuntia* subg. *Cylindropuntia*). It was first found growing on an open, gently sloping, south-facing bajada near the base of Mt. Anteojo of the Sierra de la Madera. Additional collections have extended the range to three other contiguous basins to the west and south.

Opuntia anteojoensis D. J. Pinkava, sp. nov. Frutex demissus, 0.3–1.0 m altus, intricate ramosissimus. Rami ultimi 2–3 cm longi, circa 8 mm diametro tuberculis rhombicis elevatis circa 5 mm latis, 8 mm longis. Areolae pubescentes, elongatae, inter bases tuberculorum duorum contiguorum sursum extensae, spinis principalibus porrectis solitariis ad areolas supernas pro parte maxima restrictis, subcylindraceis 2.5–7.0 cm longis, 0.7–1.0 mm diametro, nigris, apicibus porphyreis glochiadatis, vaginis transluscentibus ad apices ochraceis, spinis accessoris porphyreis utque ad 4 mm longis rarenter praesentibus, glochidiis aliquot albidis 1–2 mm longis. Flores terminales vel subterminales in ramis brevibus, solitarii vel 2–4 in fasciculis, rotati, utque ad 4 cm diametro, tepalis coloratis 10–20 luteis, mucronatis, margine undulatis vel erosis. Fructi sicci, subcylindracei, 1.5–2.5 cm longi, 10–12 mm diametro, lappacei, spinis flexilibus atrobrunneis apice aureis utque ad 20 mm longis spinosissimi, areolis trichomis aureis copiose pubescentibus, perianthio persistenti. Semina circa 10–20 per fructum, 5.0 × 4.5 × 2.0 mm, arillo cretaceo farinoso angulari.

Type: México, Coahuila, ca 21 km W of Cuatro Ciénegas on road to Esmeralda (26° 56′ N, 102° 15′ W), matorral desertico inerme, 800 m elev., sloping bajada near S face of Sierra de la Madera, 7 May 1973, *M. C. Johnston, T. L. Wendt, and F. Chiang C. 10911* (in flower). Holotype: LL. Isotypes: ASU, remainder to be distributed. Paratypes: México, Coahuila: 16 km W of Cuatro Ciénegas (26° 58′ N, 102° 10′ W), *Johnston, Wendt, and Chiang 9151* (ASU, LL); ca 6 mi W of Poso Anteojo, *Meyer s.n.* (in fruit) (ASU, DES, ENCB), *Lehto, Keil, and Pinkava P5527* (ASU, LL), *Pinkava 10512–10513* (ASU); 18.5 km S of turnoff to Sta. Sofia, Cuatro Ciénegas-Torreon highway (26° 35′ N, 102° 23′ W), *Johnston, Wendt, and Chiang 10988* (in flower) (ASU, LL); E side of Valle de Sobaco, ca. 15 air km SE of Las Margaritas (26° 24′ N, 102° 43′ W), *Chiang, Wendt, and Johnston 9466* (in fruit) (LL); 12.5 km NW of Los Colorados toward Palomas and Cuatro Ciénegas (26° 14′ N, 101° 44′ 30″ W), *Johnston, Wendt, and Chiang 11724* (ASU, LL).

Opuntia anteojoensis, endemic to the Chihuahuan Desert, appears most closely related to *O. ramosissima* Engelm. The latter occurs in the Sonoran Desert, its range centering about the lower Colorado River in Arizona, California, Nevada, and Sonora. More than 1500 km separate the known ranges of these two taxa.

Both species are represented by low, intricately branched shrubs, their branches bearing rhombic tubercles with elongate areoles extending upward between the two adjacent tubercles above, and the uppermost areoles bearing a long porrect spine. Fruits are dry, maturing as burs. The two cacti differ in that *O. anteojoensis* has raised tubercles and yellow flowers whereas *O. ramosissima* has flattened, plate-like tubercles and apricot to brown flowers (fig. 1). The stems of *O. anteojoensis* commonly bear fewer spines and in age usually become thicker than those of *O. ramosissima.*

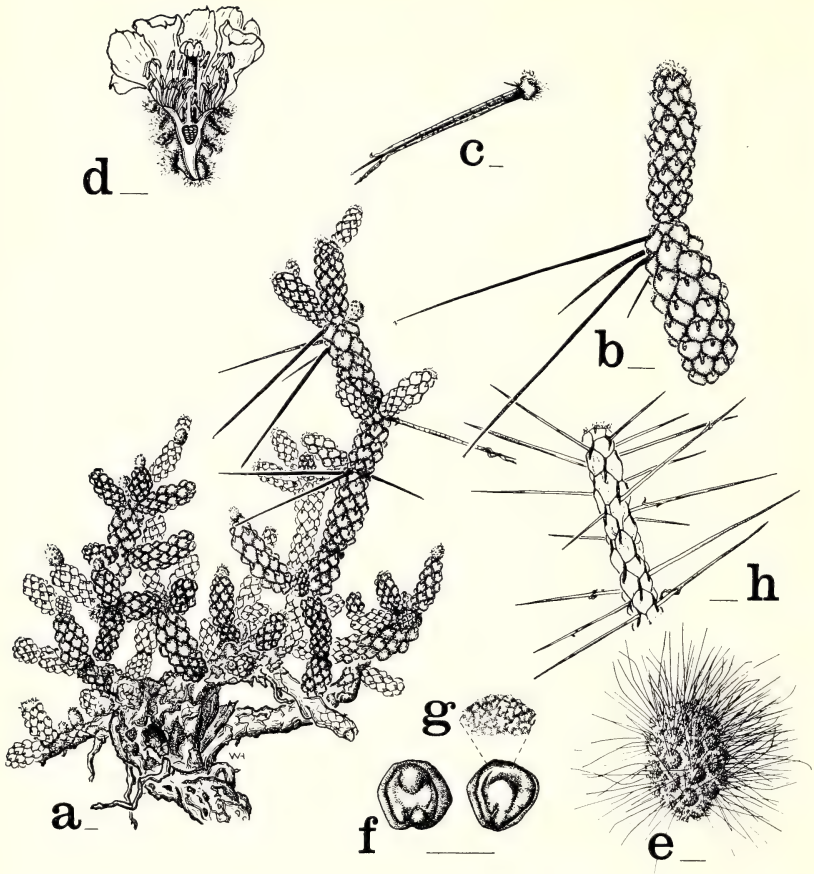

FIG. 1. *Opuntia anteojoensis.* a, habit (*Pinkava 10512*); b, stem tip enlarged (*Pinkava 10522*); c, spine and sheath (holotype); d, flower (holotype); e, mature fruit (*Meyer s.n.*); f, g, seeds (*Meyer s.n.*); h, stem tip of closely related *O. ramosissima* (*Reeves and Pinkava P11738*) illustrating detailed differences in tubercle shape, size, and arrangement. Scale line = 5mm.

ACKNOWLEDGMENTS

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Range Extension for Quercus dunnii in Central California.—*Quercus dunnii* Kell. (*Q. palmeri* Engelm.) is a divaricately branching shrub with hard, spinose-dentate leaves. It occurs in xeric chaparral or pinyon-juniper woodland in small, widely disjunct populations in Arizona, southern California, and northern Baja California. In the more xeric parts of its range, as in central Arizona, it may be associated with desert plants such as *Canotia holacantha, Opuntia engelmannii, Glossopetalon nevadense, Ephedra viridis,* and *Yucca baccata.* However, at the Peachy Canyon location in California, heretofore considered to be its northern (and western) limit, it occurs under considerably more mesic conditions with *Q. agrifolia.*

The distribution of *Q. dunnii* in Arizona is presented elsewhere (Tucker and Haskell, Brittonia 12:196–219. 1960). Its known range in Baja California extends just south of the Sierra San Pedro Mártir (R. Moran, pers. comm.: west of Agua Amarga, 1100 m, near 30° 28′ N, 115° 17′ W, *Moran 11416*). In southern California it occurs principally along the western borders of the Colorado and Mohave Deserts in Riverside, San Bernardino, and Los Angeles Counties. To the east, it first reoccurs in the Hualapai Mountains in Mohave County, Arizona. However, a late Pleistocene record has recently been discovered in the Newberry Mountains in extreme southern Nevada (Leskinen, Madroño 23:234. 1975).

In October 1974, J. R. Griffin found *Q. dunni* in Clear Creek Canyon, a tributary of the upper San Benito River in southeastern San Benito County. The locality is 36° 22′ 20″ N and 120° 43′ 50″ W; on the U.S.G.S. 15′ New Idria quadrangle it appears near the southeastern corner of section 11, T. 18 S., R. 11 E. This extends the known range of *Q. dunnii* 82 km north of Peachy Canyon, west of Paso Robles, San Luis Obispo County.

An old bulldozer trail to the Alpine mercury mine runs by the colony. The county road from Hernandez to New Idria (Clear Creek Road) passes within sight of the colony 350 m away. The main slope of Clear Creek Canyon faces northwest here, and the *Q. dunnii* shrubs are on the shady side of a ravine running down the slope at an elevation of 960 m. The surrounding vegetation is a "serpentine" chaparral dominated by *Q. durata* with lesser amounts of *Arctostaphylos glauca* and *A. pungens.* Trees of *Pinus sabiniana* are scattered in the brush. The *Q. dunnii* shrubs appear to be on an outcrop of Franciscan sediments within the generally serpentine region. The non-serpentine influence around the colony is evident by the presence of *Cercocarpus betuloides, Q. turbinella* ssp. *californica,* and *Juniperus californica. Yucca whipplei* is scattered on rocky openings, and *Chrysothamnus nauseosus* ssp. *mohavensis* is abundant along the bulldozer trail and other disturbed spots.

The *Q. dunnii* population (*Tucker 4342, 4343; Griffin 3928*) is extremely localized at Clear Creek; several dozen stems, 2–4 m tall, are involved in the main group. Several smaller individuals have started nearby, possibly since the bulldozer trail was built, and a single large spreading shrub occurs a short distance up slope. *Quercus dunnii* may grow elsewhere in Clear Creek Canyon, but if so the species must be very inconspicuous. Griffin (Fremontia 2(1):11–15. 1974; U.S. Forest Service Research Paper PSW-, in press) explored the region intensively before stumbling onto this colony.

The Clear Creek *Q. dunnii* shrubs are separated from a tiny population of the closely related species, *Q. chrysolepis,* by only 1.45 km. The *Q. chrysolepis* trees (*Tucker 3657*) also grow near Franciscan outcrops in a narrow gorge farther up Clear Creek. *Quercus chrysolepis* is essentially absent from the serpentinized portions of the San Benito Mountain region although scattered in chaparral on high ridges of the Diablo Range on non-serpentine rocks. This is as close as the two species come to co-existing of any place in California known to us. However, unlike the situation in central and southeastern Arizona, where these oaks have hybridized freely (Tucker and Haskell, op. cit.), in Clear Creek Canyon there is no evidence of introgression in either species.—J. R. Griffin, Hastings Reservation, Carmel Valley, California 93924 and J. M. Tucker, Botany Department, University of California, Davis 95616.

Chromosome Counts and a New Combination in Claytonia sect. Limnia (Portulacaceae).—The following information has come to light as a result of studies of *Claytonia sibirica* L. and its close relatives. It is being published now because it will be of interest to others working on this group of taxa and will not be included in later, more detailed papers.

Recent studies of *Claytonia* by J. R. Swanson (Ph.D. Dissertation, Univ. California, Berkeley, 1964), J. M. Miller (Syst. Bot., in press), and C. E. Fellows (unpubl.) indicate that within such species as *C. perfoliata* Donn, *C. sibirica,* and *C. spathulata* Hook. there exist a number of evolutionary entities that are currently being loosely held together taxonomically by one to several superficial characteristics. My studies of seed, pollen, and chromosome characteristics, as well as field observations on the ecology of *C. spathulata* and *C. perfoliata,* indicate that total reliance on the degree of cauline leaf fusion to group infraspecific taxa has led in the past to partially artificial assemblages. The best clue to natural relationships among the many morphologically confusing forms comprised by *C. perfoliata* (sensu lato) and *C. spathulata* (sensu lato, including *C. gypsophiloides* F. & M.) is base chromosome number. *Claytonia perfoliata* comprises a euploid series of populations based on $x = 6$ and ranging from diploid to decaploid (Swanson, *op. cit.*; Miller, *op. cit.*). Chromosome counts, including several that are unpublished, are now known for the *C. spathulata* group, and its base number is consistently $x = 8$. Diploids, with $2n = 16$, occur (Swanson, op. cit.; Lewis, Ann. Missouri Bot. Gard. 54:180. 1967; Fellows, unpubl.) and these include the taxon *C. gypsophiloides* (Nilsson, Bot. Not. 119:464–468. 1966; Fellows, unpubl.); the hexaploid level ($2n = 48$) has been found in a form of *C. spathulata* common in the Pacific Northwest (Nilsson, op. cit.; Table 1).

Correlated with chromosome base number is seed morphology in the two species complexes. *Claytonia perfoliata* seeds have a shiny "highlight" when illuminated and are smooth, the tessellate pattern of low papillae being barely visible with a hand-lens. They have a relatively large elaisome inserted in a wide notch in the

Table 1. Chromosome Counts in Claytonia. * = counts made by K. L. Chambers. Collection numbers are those of the author unless otherwise stated. Voucher for *398* is at HSC; all others are at OSC.

Claytonia rubra (How.) Tidest.
CA, Siskiyou Co., near city of Mount Shasta, *675,* $n = 6$.
OR, Josephine Co., Rough-and-Ready Creek N of O'Brien, *Chambers 2490,* $n = 6$*.
WA, Kittitas Co., 19 mi NW of Ellensburg, *512,* $n = 6$.
Claytonia perfoliata Donn, sens. lat., excluding subsp. *viridis.*
CA, Humboldt Co., 3 mi above Freshwater, *480A* and *480C,* $n = 6$; Clam Beach, *398* (offspring), $n = 12$; Titlow Hill Rd., *714,* $n = 18$.
CA, Mendocino Co., 4.0 mi from hwy. 101 on hwy. 128, *603,* $n = 18$.
CA, Napa-Lake Co. line, on hwy. 29, *599,* $n = 18$.
CA, Ventura Co., Wheeler Gorge Campground, *685* and *686,* $n = 6$.
OR, Josephine Co., Rough-and-Ready Creek N of O'Brien, *Chambers 2491,* $n = 18$*.
WA, Clallam Co., 0.5 mi W of Sequim, *J. Miller 270,* $n = 18$.
Claytonia perfoliata subsp. *viridis* (A. Davids.) Fellows
CA, Riverside Co., 1 mi N of Mountain Center, *981,* $n = 12$.
CA, San Diego Co., near Pine Valley Creek, *964,* $n = 12$.
CA, Ventura Co., near Canyon Creek, *687,* $n = 12$.
Claytonia spathulata Hook.
OR, Wasco Co., Mayer State Park, Rowena, *Chambers 2486,* $n = 24$*.

seed coat. Seeds of *C. spathulata* appear more dull-surfaced because they are evenly pebbled with minute papillae, and their elaisome is relatively much smaller than that of *C. perfoliata*. These differences are well illustrated by drawings on pages 244 and 248 in *Vascular plants of the Pacific Northwest,* part 2 (Hitchcock et al., 1964).

Plants of the *C. spathulata* group typically occupy fully open sites in sand or gravelly soil, or on mats of moss on bare rocks. Their stems and leaves are usually gray-glaucous. The habitats of *C. perfoliata* include many types of open or shaded conditions and soils ranging from dry and sandy to moist and highly organic. Especially when in shade, plants of *C. spathulata* are green or reddened with betacyanin pigments and are not glaucous. These habital differences are variable and difficult to quantify and are less useful than seeds or chromosome number in assigning taxa to one or the other of these species complexes.

A long-recognized taxon of Southern California, which botanists have consistently associated with the *C. spathulata* group, is *C. spathulata* var. *viridis* (A. Davids.) Munz. Chromosome counts of three widely separated populations (Table 1) show that it is a tetraploid on a base of $x = 6$. These plants have a seed morphology similar to that of *C. perfoliata*, and they occur often in shaded habitats and are nonglaucous and green (as the varietal epithet implies). To indicate the natural relationship of this entity to *C. perfoliata,* I propose the following new combination:

Claytonia perfoliata Donn subsp. **viridis** (A. Davids.) Fellows, comb. et stat. nov.—*Montia spathulata* var. *viridis* A. Davids., Bull. S. Calif. Acad. Sci. 5:61. 1907.—*M. exigua* var. *viridis* Jepson, Fl. Calif. 1:473. 1915.—*Claytonia exigua* var. *viridis* v. Poelln., Feddes Repert. Spec. Nov. Regni Veg. 30:306. 1932.—*Limnia viridis* Rydb., N. Amer. Fl. 21:313. 1932.—*C. spathulata* var. *viridis* Munz, Fl. S. Calif. 713. 1974. TYPE: California, San Gabriel Mountains, Big Rock Creek, pine woods, 6 Jun 1906, *Hasse & Davidson 1507*. Holotype: LAM!.

Field work for this study was supported in part by grant GB-39232 from the National Science Foundation. I thank Dr. K. L. Chambers for assistance with the manuscript.—CHARLES E. FELLOWS, Department of Botany, Oregon State University, Corvallis 97331.

NOMENCLATURAL NOTES ON CLAYTONIA SPATHULATA.—The protologue for *Claytonia spathulata* Dougl. ex Hook. (Fl. Bor. Amer. 1:226. tab. 74. 1832) includes citation of syntypes, "North-West coast of America. *A. Menzies, Esq.* in Herb. nostr.—In the vallies of the Rocky Mountains, common. *Douglas.*" It appears that no one has yet taken the formal step of designating a lectotype for this name, although various authors have implied that one or the other of the cited collections is the "type". Robinson (in Gray, Syn. Fl. N. Amer. 1:275. 1897) said ". . . first coll. by *Douglas*". Rydberg (N. Amer. Fl. 21:313. 1932) gave the type lacality as "Rocky Mountains [Canada]". R. S. Ferris (in Abrams, Illus. Fl. Pac. States 2:127. 1944) says simply "Canada". Hitchcock (Vas. Pl. Pac. N. W. 2:246) states, "*Menzies,* 'North-West coast of America,' is the first of two collections cited". Through the courtesy of the Royal Botanic Gardens, Kew, we have examined the type sheet of *C. spathulata* from the Hooker Herbarium (photograph, OSC), and we would like to present the following comments regarding typification of this name.

The top three individuals on the sheet in *Herbarium Hookerianum* are associated with a field label by David Douglas, which reads, "Claytonia *spatulata* (sic!) D. D. In the vallies of the Rocky Mountains. Common." On the sheet beside this label, Hooker (we assume) has written the phrase "v. C. exigua Torr. & Gr.". Above the specimens there is written, anonymously, "These are the plants illustrated and described as C. spathulata." In the middle of the sheet are two other collections; one is a single rather fragmented and depauperate individual beneath which is written (presumably by Hooker), " 'Claytonia.' Sandwich isles. A. Menzies. (or N. W. C of Am)". To the right of this is a very robust individual, by which Hooker wrote, "C. spathulata β. Douglas California". At the bottom of the sheet are two less robust plants, without collector or locality, bearing Hooker's annotation, "C. spathulata γ. v. etiam C. gypsophiloides".

We propose that the largest of the three plants in the Douglas collection labeled "In the vallies of the Rocky Mountains" be designated as the lectotype of *Claytonia spathulata.* These plants match very well both the description and the illustration given in the Flora Boreali-Americana, whereas Menzies' plant (although undoubtedly representing the species *C. spathulata*) is in poor condition and bears two alternative locality designations. That the name itself was suggested by Douglas, in manuscript, is also pertinent. It is interesting that in neither the drawing nor the written description is there a mention of any connation between the cauline leaves of *C. spathulata,* although in the Pacific Northwest it is usual for plants of this species to show some such fusion. Careful examination of the lectotype indicates that the leaves are fused on one side for a distance of about 0.5 mm, and on Menzies' plant, one leaf pair shows 1 mm of fusion.

Through the kindness of the Director, Royal Botanic Gardens, we received permission to make a pollen preparation of the lectotype plant of *C. spathulata.* This slide, which is on file at Kew, shows that most of the grains have irregular aperture patterns of a syncolpate type. Most common is the occurrence of two annular colpi encircling opposite poles of the grain, these colpi often being cross-connected by one or two colpi on one side. Tricolpate and hexacolpate grains are also present. Nilsson (Grana Palynologica 7:229. 1967) stated that *C. spathulata* "is in reality 3-colpate, but it often has grains with an irregular number of colpi". Our own studies of *C. spathulata* pollen indicate that in the diploid types the grains are regularly 3-colpate, but that in the hexaploid type ($2n = 48$) that is common in the Pacific Northwest, irregularly syncolpate grains occur that are like those seen from the lectotype. Palynological evidence suggests, therefore, that the lectotype represents a polyploid form of the species.

It is a puzzle as to exactly where Douglas made his collection of *C. spathulata,* since as far as we can determine, the logical choices—namely, the valleys of the upper Columbia River, in what are now the Canadian Rockies—are outside the range of this taxon. Douglas would have encountered the plant on the coast and along the lower Columbia River to perhaps as far east as what are now Gilliam and Morrow Counties, Oregon. One might speculate that Douglas meant the Cascades, rather than the Rockies, or that he was referring to the Blue Mountains, which he visited on a trip south out of Walla Walla. We cannot offer any good answer to this question.

The collection by Douglas, from California, that Hooker annotated as "C. spathulata β." is the holotype of the taxon *Claytonia spathulata* var. *major* Hook. & Arn. (Bot. Beech. Voy. 344. 1839), a name that has been almost universally overlooked in the synonymy of this species (the only citation we found is in the Gray Herbarium Card Index). The type is a robust plant with very numerous linear leaves, lanceolate cauline leaves that are 10–18 mm long and connate on one side up to 5 mm, and petals that are up to 5 mm long. A probable isotype is at CGE.

In the Botany of Beechey's Voyage (loc. cit.) Hooker and Arnott described a third variety of *C. spathulata,* making a combination that also has been overlooked by most later bibliographers: *Claytonia spathulata* var. *exigua* (T. & G.) Hook. & Arn., based on *C. exigua* of Torrey and Gray (Fl. N. Amer. 1:200. 1838), the type being a collection by Douglas from California. As recently as 1974, Munz (Fl. So. Calif. 713) attributed this combination to Piper (Contr. U. S. Natl. Herb. 11:250. 1906); however, the infraspecific combinations made by Piper in his Flora of the State of Washington are better treated as being subspecies (note, for example, on p. 572, "*Aster campestris suksdorfii* subsp. nov.").—Charles E. Fellows and Kenton L. Chambers, Department of Botany, Oregon State University, Corvallis 97331.

Empetrum hermaphroditum (Empetraceae) in Humboldt County, California.—A small population (ca 8 m^2) of *Empetrum hermaphroditum* (Lange) Hagerup was recently discovered along the coast of Humboldt County within Trinidad Beach State Park, 29 Mar 1975, *G. S. Lester 600* (HSC); 4 Apr 1975, *G. S. Lester 604* (RSA, CAS, JEPS, UC). The plants are growing at Megwil Point on Elk Head just N of Trinidad (22 km N of Eureka). Here *Empetrum* forms thick, distinctive dark green mats and occupies the NW facing portion of a standstone bluff with regionly abundant shrubs, *Vaccinium ovatum* Pursh, *Gaultheria shallon* Pursh, and *Garrya elliptica* Dougl. This locality is 81 km S of Point St. George, Del Norte County, the only recently known *Empetrum* site in California. Intensive surveys over the last two years suggest that *Empetrum* has been extirpated in the Point St. George region.—Gary S. Lester, Department of Biology, Humboldt State University, Arcata, California 95521.

Vascular Plants of Montane Coniferous Forest in San Bernardino Mountains, California.—In our work on the impact of oxidant air pollution we established a series of eight riparian zone transects and 101 upland plots in the montane coniferous forest of the San Bernardino Mountains. Three hundred thirty-seven species of vascular plants representing 224 genera and 55 families were collected from these transects and plots. Three hundred fifteen of these were native and twenty introduced. Twenty-six species are endemic to the San Bernardino Mountains and fifteen are considered as rare or endangered by the California Native Plant Society. This collection includes 83 species not listed in Parish's (*Plant World* 20: 208–223. 1917) enumeration of the flora of the San Bernardino Mountains and three species not previously reported by Munz (*A flora of Southern California.* 1974) as occurring in Southern California. Voucher specimens are preserved in the herbarium of the Department of Forestry and Conservation, University of California, Berkeley.

A list of taxa collected in this study and including those listed by Parish, but not collected by us, may be obtained from the Department of Forestry and Conservation, 145 Mulford Hall, University of California, Berkeley, CA 94720. This list contains habitat information and indicates which taxa are introduced.—Joe McBride, Tana Hill, Randy Milliken, and Nikki Laven, Departments of Forestry & Conservation and Conservation of Natural Resources, University of California, Berkeley 94720.

Literature of Interest

Native trees of the Sierra Nevada. By P. Victor Peterson and P. V. Peterson, Jr. 147 pp., 12 color pl. 1975. California Natural History Guides: 36. University of California Press, Berkeley. $3.96 (paperback). Contains descriptions, ranges, drawings, self-guided itineraries.

A field guide to the common and interesting plants of Baja California. By Jeanette Coyle and Norman C. Roberts. xi + 206 pp. 1975. Natural History Publishing Co., P.O. Box 962, La Jolla, California 92037. $8.50 (paperbound); $11.00 (hardcover).

The Alaska-Yukon wild flowers guide. By editorial staff of *Alaska* magazine, H. A. White, editor. viii + 218 pp. 1974. Alaska Northwest Publishing Co., Anchorage. $7.95. Color photographs of common and/or interesting wildflowers, giving scientific and common names (with indices), a brief statement of habitat and range, habit sketch, and color photographs (half to full page); about 160 species treated.

Geology field guide to Northern California. By John W. Harbaugh. xv + 123 pp., illus. 1974. Wm. C. Brown Co., Dubuque, Iowa. $2.95.

Historical atlas of California. By W. A. Beck and Y. D. Hasse. Unpaged, but ca. 200 pp. 1974. University of Oklahoma Press, Norman.

REVIEW

Aquatic and wetland plants of southwestern United States. By Donovan S. Correll and Helen B. Correll. 2 vols., xv + 1777 pp., frontispiece, 784 figs., map. Stanford University Press, Stanford, California. 1975. $37.50. Originally published in 1972 by United States Environmental Protection Agency.

Vascular plants associated with permanently or seasonally wet habitats in Arizona, New Mexico, Oklahoma, and Texas are systematically accounted for in these volumes. Because the authors delimited the area treated politically instead of floristically, the manual will be useful for research in bordering regions, especially to the east.

The authors' preface indicates criteria used for inclusion/exclusion of taxa and includes a brief account of the history of the project. Fairly detailed characterizations of included habitats are given in the Introduction along with general remarks about aquatic and semiaquatic vascular plants including economics of controlling weedy species and the relationships between vascular plants and water pollution.

The manual itself provides keys for identification of families, genera, and species. Typical entries for species include: accepted name; common name(s), where appropriate; brief, detailed description; statement of distribution in Southwest; flowering time; statement of general distribution; and, frequently, additional notes on biological and/or economic importance of the taxon. Many of the descriptions are supplemented by line drawings, many of which were published in various other manuals of aquatic plants.—John L. Strother, Botany—University Herbarium, University of California, Berkeley 94720.

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DISJUNCTION OF GREAT BASIN PLANTS IN THE NORTHERN SIERRA NEVADA

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The montane zone of the Sierra Nevada is rich in number and diversity of floristic elements. Taxa that have had different geographical origins and migrational histories are found within adjacent communities. Many subalpine and alpine taxa in the Sierra show their closest relationships to floras of the cool, mesic areas of the Cascades and Rocky Mountains (Sharsmith, 1940; Smiley, 1915; Pemble, 1970); others are related to the warm, dry areas of adjacent lowlands (Chabot and Billings, 1972; Went, 1948).

Klyver (1931), Major and Bamberg (1963), Neilson (1971), and Smith (1973) noted typically Great Basin taxa in xeric sites west of the crest of the Sierra Nevada. These taxa often are disjunct by considerable distances from their nearest occurrences to the east, being separated by expanses of mesic forest vegetation.

At Carson Pass, Alpine County, California, dry site vegetation is strikingly similar to that occupying upland sites throughout much of Nevada. This similarity will be described and discussed in relation to past environmental conditions that may have been responsible for the migration and subsequent disjunction of the Great Basin floristic element on the crest and west slope of the northern Sierra Nevada and in cismontane California in general.

Carson Pass

Carson Pass lies astride the crest of the Sierra Nevada. Several high peaks in the Carson Range exceed 3000 m elevation at Carson Pass: Steven's Peak (3064 m), Red Lake Peak (3066 m) and Round Top (3163 m). Carson Pass is located in the low saddle between the two last-named peaks at 2612 m. Immediately to the east is Hope Valley, a broad, lowland basin at 2000–2100 m, then another ridge rising to above 3000 m. This ridge is cut by the canyon of the West Fork of the Carson River to the level of Hope Valley and leads to the floor of the Great Basin to the east. North of Carson Pass on the east side of the crest lies Lake Tahoe at 1930 m, separated from Carson Pass by ridges rising to 2850 m.

Climatically, the region is typical of subalpine localities on the west slope of the Sierra Nevada, but records are scanty.

Geologically, the Carson Pass area is quite complex. Intrusive granitic and extrusive volcanic rocks compose the majority of the substrates.

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There are small exposures of intrusive volcanic and metasedimentary formations. Metamorphism has altered many of the regional formations (Crawford, 1969). Moderate folding and faulting have placed contrasting substrates in juxtaposition.

Vegetation types found at Carson Pass are typical of timberline elevations in the Sierra. Open forests of *Pinus albicaulis,* denser forests of *Abies magnifica, Tsuga mertensiana,* and *Pinus monticola,* mesic meadow, and alpine associations form a complex mosiac. Xeric areas of considerable extent occur chiefly on southerly exposures underlain by Miocene and Pliocene andesitic mudflow breccias.

Disjunct Taxa

The flora of the subalpine and alpine zone at Carson Pass is diverse: 580 taxa of vascular plants have been collected from above the 2440 m contour within a radius of 10 km (Taylor, 1974). The total flora of the area shows high overall similarity to those of nearby regions, such as the Lake Tahoe basin (Smith, 1973) or Tuolumne Meadows (Howell, 1944; Clausen, 1969; Pemble, 1970). However, there is a sizable Great Basin floristic element at Carson Pass that is not as well developed in the above locations or other areas in the Sierra for which plant lists are available (e.g., Norden: Howell, 1943; Convict Creek basin: Major, 1966; Pemble, 1970; Rock Creek Lake Basin: Peirson, 1938, 1942; Mineral King: Howell, 1952; Rice, 1969).

Fifty-six disjunct taxa (Table 1) characteristic of the semiarid shrub-steppe and pinyon woodland associations of the Great Basin can be considered to compose the nucleus of this disjunct element. All have the major part of their distribution in the Great Basin province (Fenneman, 1928). Vouchers are deposited in DAV or CAS; collection information and nomenclature can be obtained from Smith (1973) and Taylor (1974).

Some of the taxa in Table 1 are elevationally disjunct by as much as 1000 m above their nearest populations 20 km to the east. Several others have more notable disjunctions.

Betula occidentalis: The nearest populations to the Woods Lake locality at Carson Pass (Smith, 1973) are about 200 km to the south in the Owens Valley, Inyo County (Davidson, 1911; Griffin and Critchfield, 1972) and at mid-elevations in the upper drainages of the Kings and Kern rivers in the southern portion of the Sierra (Rockwell and Stocking, 1969) and 250 km northeast on the uplands surrounding Mt. Shasta in Siskiyou County (Griffin and Critchfield, 1972).

Crataegus columbiana: This is disjunct by about 300 km to the south of the nearest known populations on the Modoc Plateau, northeastern California.

Townsendia scapigera: Populations at Carson Pass are separated by 65 km from nearby stations in the Virginia Range, Nevada, and the Sweetwater Mountains, Mono County, California.

TABLE 1. DISJUNCT TAXA FROM THE GREAT BASIN IN THE ALPINE AND SUBALPINE ZONES AT CARSON PASS.

TREES

Pinus monophylla, Betula occidentalis

SHRUBS

Amelanchier utahensis, Artemisia arbuscula, A. tridentata ssp. *vaseyana, Cercocarpus ledifolius, Chrysothamnus nauseosus* ssp. *albicaulis, C. viscidiflorus, Crataegus columbiana, Eriogonum microthecum, Purshia tridentata, Ribes velutinum, Rosa woodsii* var. *ultramontana, Tetradymia canescens*

HERBS

Antennaria dimorpha, Allium parvum, Agoseris glauca var. *monticola, Aster adscendens, Astragalus purshii* var. *lectulus, A. whitneyi, Brickellia oblongifolia* var. *linifolia, Balsamorhiza sagittata, Cirsium utahense, Chenopodium overi, Crepis acuminata, C. bakeri, C. modocensis* ssp. *subacaulis, Castilleia linariaefolia, Chamaesaracha nana, Erigeron aphanactis, E. linearis, E. nevadincola, E. tener, E. eatonii* ssp. *plantagineus, E. breweri* var. *porphyreticus, Haplopappus acaulis, H. bloomeri, Hydrophyllum capitatum* var. *alpinum, Leptodactylon pungens* ssp. *pulchriflorum, Lupinus caudatus, Lygodesmia spinosa, Melica stricta, Mentzelia dispersa, Mimulus densus, Navarretia breweri, Poa cusickii, P. juncifolia, P. nevadensis, Phoenicaulis cheiranthoides, Phacelia humilis, Phlox covillei, Senecio canus, Scrophularia desertorum, Townsendia scapigera, Viola beckwithii, Zigadenus paniculatus*

XERIC VEGETATION

The disjunct taxa (Table 1) are largely restricted to dry, rocky or shallow soil sites at Carson Pass, where they contribute to two distinctive associations, both of which have admixtures of Great Basin and Sierran elements.

Sites at lower elevations (2500–2700 m) on southerly or easterly exposures with slightly acid soils (pH 5.6–6.4) support an open woodland (< 50% canopy coverage) of *Juniperus occidentalis* ssp. *australis*, with scattered *Populus tremuloides* and *Pinus contorta* var. *murrayana*. The associated low shrub layer (< 1 m) is composed of *Artemisia tridentata* ssp. *vaseyana, Ribes cereum, Symphoricarpos vaccinioides, Chrysothamnus nauseosus* ssp. *albicaulis, Holodiscus microphyllus*, and *Ceanothus cordulatus* along with perennial herbs such as *Wyethia mollis, Balsamorhiza sagittata*, and *Erigeron breweri* var. *porphyreticus*. This *Juniperus occidentalis* ssp. *australis/Artemisia tridenta'a* ssp. *vaseyana* association is found on fairly deep (1.0–1.2 m), well-drained soils derived from granitic or coarse-grained volcanic parent materials (Rogers, 1974). Snow cover is nearly continuous from November to late April, and adequate soil moisture is available until early summer.

The second association inhabits higher elevations (2600–3000 m) on nearly neutral (pH 7.0–7.8), shallow (< 0.5 m), rocky soils derived from volcanic rocks. This low (< 0.5 m tall) vegetation is composed chiefly of the shrubs *Artemisia arbuscula, Haplopappus acaulis, Leptodactylon pungens* ssp. *pulchriflorum, Amelanchier utahensis*, and *Tetradymia canescens*. The numerous perennial herbs in this association

contribute little to the sparse (< 25%) cover. This *Artemisia arbuscula/ Haplopappus acaulis* association occupies the driest, most wind-exposed sites. Snow cover is intermittent to nearly absent in winter, and water availability is low through the year.

In overall physiognomy, structure, or composition these two associations are strikingly similar to the *Pinus monophylla/Juniperus osteosperma* woodland and *Artemisia tridentata* scrub vegetation types of the Great Basin, such as those described by Daubenmire (1971) and Franklin and Dyrness (1973) for eastern Washington, by Lewis (1971) and Loope (1969) for the Ruby-East Humboldt Mountains of eastern Nevada, and by Blackburn et al. (1968, 1969), Billings (1945, 1951), and Beeson (1974) for central Nevada. Some of the stands described by Daubenmire and located 1000 km to the north are nearly identical in composition to stands at Carson Pass.

Migrational History

Members of the Great Basin floristic element at Carson Pass are almost exclusively limited to the vegetation types described above. The question arises as to when and how these disjunct communities came to occupy azonal sites in the northern Sierra Nevada.

There is low probability that each of the disjunct taxa was dispersed to Carson Pass independently, subsequently reconstituting a disjunct phytosociological assemblage; rather, it is more likely that they migrated as an intact vegetation unit.

These disjunct communities are currently isolated from similar neighboring populations by expanses of mesic forest and meadow vegetation. The thesis advanced here is that these communities migrated to Carson Pass and into other areas west of the Sierran crest when past climate was significantly different from that of the present. Subsequent climatic changes have forced their general restriction to the east, leaving relict patches on compensatory, azonal sites.

The course of climatic change for North America since the last glacial epoch of the Pleistocene is fairly well documented in the literature, although data for California are scarce. Full glacial climates were cooler than at present by 8–9°C mean annual temperature (MAT) (Wright and Frey, 1965; Flint, 1973) and had lower evapotranspiration rates resulting in greater moisture availability, although overall precipitation may have been reduced as much as 10–15 percent (Galloway, 1970). A gradual warming trend began at the close of the last ice advance, 12,000–14,000 years B.P., and continued until approximately 3500 years B.P., followed by a minor cooling trend up to the present. The intermediate period of warming (termed the Xerothermic period) extended from about 6600–3500 years B.P. and was characterized by reduced precipitation and by MAT's 3–5°C higher than at present.

Comparison of climatic characteristics of selected weather stations in

TABLE 2. COMPARISON OF THE CLIMATIC CHARACTERISTICS OF SELECTED STATIONS REPRESENTING UPLAND VEGETATION TYPES OF NEVADA WITH THE TWIN LAKE STATION AND THE INFERRED CLIMATE OF THE ARTEMISIA ARBUSCULA/HAPLOPAPPUS ACAULIS ASSOCIATION AT CARSON PASS. MAT = mean annual temperature; AR = annual range of mean monthly temperatures; TW = mean monthly temperature warm month; TC = mean monthly temperature cold month; PPT = precipitation. Values are in °C and mm of water; data from report by U. S. Department of Commerce (1972).

Station	MAT	AR	TW	TC	PPT
		Carson Pass			
	Artemisia arbuscula/Haplopappus acaulis scrub				
Twin Lakes (projected)	3.1	16.1	12.3	—3.8	655
	Pinus contorta var. *murrayana* forest-*Carex/Salix* meadow				
Twin Lakes	3.9	17.6	12.8	—4.8	1180
		Nevada			
	Pinus monophylla/Juniperus osteosperma woodland				
Austin	8.6	22.6	21.2	—2.0	302
Contact	8.0	23.6	20.6	—3.0	212
Elko	7.4	26.0	20.8	—5.2	230
Ely	6.9	24.8	19.7	—5.1	212
Wells	7.1	25.8	20.7	—5.1	243
Virginia City	8.8	21.2	21.6	—0.7	265
Lehmann Caves	8.6	23.1	21.7	—1.4	324
	Artemisia tridentata scrub				
Reno	9.1	20.4	19.8	—0.8	182
Battle Mountain	8.6	25.1	21.8	—3.3	176
Minden	9.8	21.4	20.8	—0.6	219
Carson City	10.0	20.9	20.9	0.0	282

Nevada with records from the Twin Lakes (Caples Lake) station at Carson Pass is given in Table 2. The Twin Lakes station is located in an open, seasonally wet meadow covered with clones of *Salix lemmonii* interspersed in a matrix of *Carex rostrata, C. nebrascensis, C. aquatilis,* and *Deschampsia caespitosa* surrounded by closed-canopy forest of *Pinus contorta* var. *murrayana.* Temperature records collected by me during 1971–1974 for a nearby locality (1.5 km northwest of the Twin Lakes station) dominated by *Artemisia arbuscula* and *Haplopappus acaulis* are slightly cooler by an average of 1°C, although comparable to the values for the Twin Lakes station. Precipitation falling as snow on the dry, windswept slopes dominated by the *Artemisia/Haplopappus* association where many of the disjunct taxa occur is reduced by 50–70 percent of that recorded at the Twin Lakes station. The climate given for the *Artemisia/Haplopappus* association is inferred from the Twin Lakes long-term record by taking this precipitation loss into account. The MAT at Twin Lakes is 3.9°C, with an annual range of mean monthly temperatures (AR) of 17.6°C. Temperatures given in Table 2 for the *Artemisia/Haplopappus* association are lapse-rate projections from the Twin Lakes station based on 4 years of record. Great Brasin stations shown in Table

2 have MAT values from 6.9 to 10.0°C. and AR values from 20.4 to 26.0°C. An increase of 4–5°C in MAT (without significant changes in AR) and lowered precipitation during the Xerothermic Period would produce a climate at Carson Pass more similar to the present climate of the Great Basin and could account for the observed disjunctions. Comparison of the annual water balance (Thornthwaite, 1948; Black, 1966) at the Twin Lakes station and the inferred water balance for the *Artemisia/Haplopappus* association at Carson Pass with selected stations in Nevada is given in Table 3. The annual water balance for the *Artemisia/Haplopappus* association assumes mean monthly temperatures 1.0°C cooler than the Caples Lake station, with 50 percent of the precipitation falling as snow lost as a result of wind redistribution and deflation of the snowpack and 50 mm of soil water storage. Regimes for the Twin Lakes station at Carson Pass and the Nevada stations assume a soil water storage of 100 mm. Also given in Table 3 is the inferred regime of the *Artemisia/Haplopappus* habitat at Carson Pass with a Xerothermic MAT of 4°C higher than at present, reducing zonal precipitation 20 percent, with the same loss of snow-derived moisture and the same soil

TABLE 3. COMPARISON OF THE PRESENT ANNUAL WATER BALANCE REGIME OF THE ARTEMISIA/HAPLOPAPPUS ASSOCIATION, THE TWIN LAKES STATION AT CARSON PASS, AND SELECTED STATIONS REPRESENTING UPLAND VEGETATION TYPES OF NEVADA WITH THE INFERRED XEROTHERMIC WATER BALANCE OF THE ARTEMISIA/HAPLOPAPPUS HABITAT AT CARSON PASS. PE = potential evapotranspiration; AE = actual evapotranspiration; WS = snowmelt run-off; WD = annual water deficit. Values are in mm of water. All calculations assume 100 mm of soil water storage except those for the *Artemisia/Haplopappus* association.

Station	PE	AE	WS	WD
		Carson Pass		
		Artemisia arbuscula/Haplopappus acaulis scrub		
Twin Lakes (projected)	451	222	433	229
Twin Lakes Xerothermic (+4°C MAT)	564	252	384	312
		Pinus contorta var. *murrayana* forest-*Carex/Salix* meadow		
Twin Lakes	471	283	897	188
		Nevada		
		Pinus monophylla/Juniperus osteosperma woodland		
Austin	601	269	33	333
Contact	598	212	0	387
Elko	590	222	8	369
Ely	567	212	0	356
Wells	580	212	31	368
Virginia City	588	214	51	374
Lehmann Caves	604	285	39	319
		Artemisia tridentata scrub		
Reno	619	182	0	437
Battle Mountain	616	176	0	440
Minden	635	212	8	428
Carson City	641	215	67	426

water storage. The inferred Xerothermic water balance regime and climate for the driest sites at Carson Pass are very similar to present day conditions at upland sites in the Great Basin.

A warmer climate during the Xerothermic period would be favorable to migration of Great Basin elements into the central Sierra Nevada west of the crest. Warmer, south-facing or east-facing slopes with their characteristically shallow soils would be the most accessible habitats for Great Basin vegetation. Xeric vegetation types present at Carson Pass may therefore be relicts of Xerothermic expansion of Great Basin vegetation westward and upward into the Sierra Nevada. They appear to have persisted in compensatory sites where competition from more mesic forest and meadow vegetation is reduced.

Detling (1953, 1958, 1961) and Hickman (1968) presented evidence for a similar Xerothermic intrusion of xeric vegetation from eastern and southern sources into mesic areas of western Oregon. Similarly, Great Basin elements from the volcanic plateaus of Modoc and Siskiyou counties extended into the high mountains of the North Coast Ranges during the Xerothermic. Taxa such as *Artemisia arbuscula, Symphoricarpos vaccinioides, Arenaria congesta, Purshia tridentata, Crepis acuminata, Erigeron eatonii, Paeonia brownii, Allium parvum, Astragalus purshii* var. *lectulus,* and *Leptodactylon pungens* ssp. *pulchriflorum* are recorded from azonally dry sites in the Klamath-Trinity region (Ferlatte, 1974; Muth, 1967; Ground, 1972). Axelrod (1966) identified a parallel Xerothermic expansion of warm desert vegetation into coastal southern California and the South Coast Ranges.

A Xerothermic expansion hypothesis cannot explain the disjunction of all Great Basin plants known to occur in cismontane areas of California, however. Elements of *Pinus monophylla/Juniperus californica* woodland extend westward well into the South Coast and Transverse ranges in southern California (see Axelrod, 1966, p. 50). *Artemisia tridentata* occurs in the hills surrounding Coalinga, in the inner South Coast Ranges of Fresno County at elevations of 400–700 m (Weiler, 1966). These distributions were undoubtedly achieved during the last full-glacial period, as evidenced by macrofossils of *Pinus monophylla* and *Juniperus californica* in oil-seeps on the floor of the San Joaquin Valley at McKittrick, Kern County (Mason, 1944) dated at 38000± 2500 radiocarbon years B.P. (Berger and Libby, 1966). *Pinus monophylla* is found in several scattered locations at mid-elevations on the west slope of the Sierra Nevada. The Kings River population described by Howell (1961) from near Tehipite Valley is found on dry, rocky, south-facing slopes amidst montane chaparral vegetation and is associated with other Great Basin taxa including *Cercocarpus intricatus, Artemisia tridentata, Carex filifolia, Stipa speciosa, Phacelia cryptantha,* and *Eriogonum saxatile* and with the desert elements *Yucca whipplei* and *Garrya flavescens* var. *pallida.* Similar sites in the Tuolumne River canyon at Hetch Hetchy support *Pinus monophylla, Chrysothamnus*

nauseosus ssp. *albicaulis, Artemisia tridentata,* and *Erigeron breweri.* Harwell (1937) felt these west slope locations for *Pinus monophylla* represented aboriginal introductions, but this seems less likely when the number of associated disjuncts is considered. A more likely explanation would have these populations established in the late Pleistocene by migration without human assistance along the western foothills of the Sierra Nevada from populations known to exist in the southern San Joaquin Valley at the time (Mason, 1944).

The wide amplitude of climatic fluctuations during the late Pleistocene must have had a large effect on the abundance of organisms (Wright and Frey, 1965; Flint, 1973). The disjunction of the Great Basin floristic element at high elevations on the west slope of the northern Sierra Nevada is best explained by a westward expansion during the warm, dry Xerothermic Period.

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THE BIGCONE DOUGLAS-FIR—CANYON LIVE OAK COMMUNITY IN SOUTHERN CALIFORNIA

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Little is known about the ecology of bigcone Douglas-fir [*Pseudotsuga macrocarpa* (Vasey) Mayr]. Its relations to tree associates, soils, topography, and habitat are at best poorly understood. Whether or not bigcone Douglas-fir occupies a dominant or subordinate position within its habitat is not well known. Is it regenerating and invading new areas vigorously, holding its own, or losing ground?

Various workers have described the location, silvics, and habitat of bigcone Douglas-fir. Mason (1927) included bigcone Douglas-fir in his California Coast Range Forest, considering it an endemic and relict species. Sudworth (1908) described the natural range of the species as being delimited by lack of moisture at low elevations and by severity of climate at high ones. Furthermore, the species grows on sites too shallow, rocky, or dry for most other conifers.

In his study of vegetational types of the San Bernardino Mountains, Horton (1960) considered bigcone Douglas-fir to be a member of two vegetation types: (1) a Live Oak Woodland and (2) a bigcone Douglas-fir type. The Live Oak Woodland type usually is found on north slopes, where canyon live oak (*Quercus chrysolepis* Liebm.) predominates, although scattered individuals of bigcone Douglas-fir are often found. Bigcone Douglas-fir dominates in its type, but canyon live oak usually is present. Dominance of bigcone Douglas-fir often is reduced by fire. "Those portions of the bigcone Douglas-fir forest that are destroyed are

replaced by live oak woodland or live oak chaparral and the return of the bigcone Douglas-fir probably requires centuries" (Horton, 1960).

Gause (1966) pointed out the necessity of shade for bigcone Douglas-fir seedling establishment such that with time, continuous shade becomes a liability. A span of 40–70 years commonly is required for this species to penetrate through 5 to 9 m overstories of canyon live oak.

Methods

We sampled bigcone Douglas-fir throughout much of its range during 1966–1970. Sample locations ranged from near Tejón Pass (Los Angeles County) to near its southerly limit in California in the Agua Tibia Mountains (San Diego County), and from the San Bernardino Mountains to Tejón Pass and the west slopes of the Santa Ana Mountains. The known elevational range (280 to 2400 m) of bigcone Douglas-fir also was spanned intentionally by the samples. Altogether, 16 locations (stands) were chosen (fig. 1).

At each stand, from 4 to 12 rectangular transects 1.8 m wide and 30.5 m long were established. At least one bigcone Douglas-fir had to be

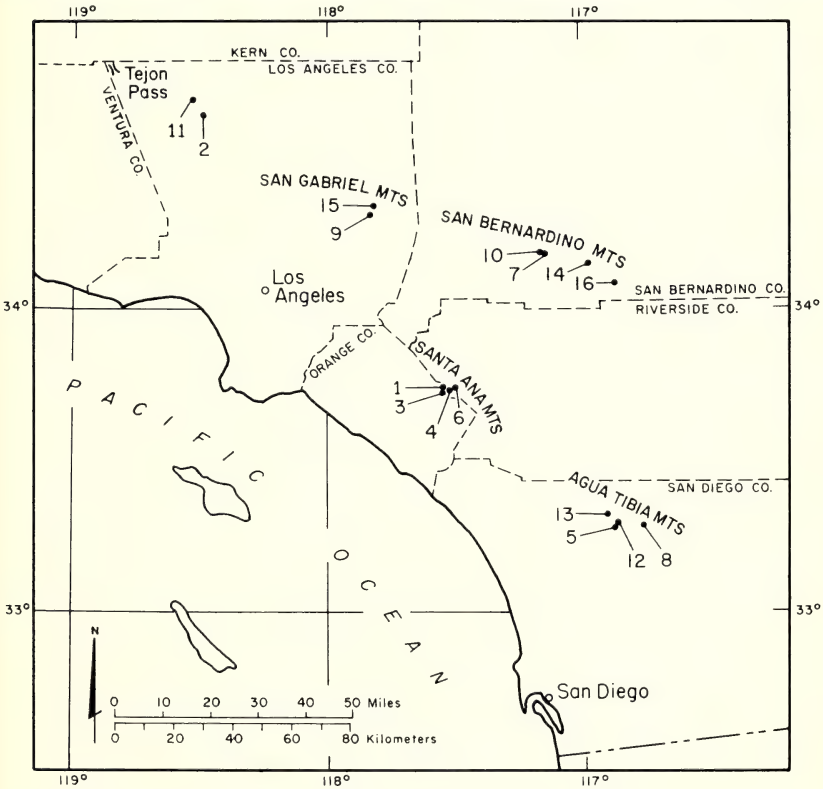

Fig. 1. Location of sampled bigcone Douglas-fir stands. (Stand numbers increase with increasing elevation.)

present on each transect. Transects were chosen, albeit arbitrarily, so that the tree community about bigcone Douglas-fir would have the best chance of being represented. Although edge effects and ecotones were avoided when recognized, the transects were located without a preconceived notion of what the community would be.

The number and orientation of the transects depended on vegetation and topography. A stand in a narrow canyon was sampled best by a few transects angled obliquely to the canyon floor. Vegetation at the bottom of a sloping hillside was measured by additional transects, one or two of which would be joined together lengthwise. Where the terrain was less steep and the vegetation more open, we selected a larger number of transects. Here their orientation resembled line transects from 122 to 183 m long. Altogether, 90 transects were established.

All regeneration (seedlings from 1.0 to 30.5 cm tall), advance reproduction [plants from 3.7 cm tall to 2.5 cm in diameter at breast height (d.b.h.) 1.4 m above mean ground line], and trees (2.8 cm d.b.h. and larger) were recorded along each transect. Data were converted to density and basal area for each stand. Subjective data included presence of acorns, cones, and woody plants, number of stems per clone, and seedling growth rates.

Climate of the canyons and slopes where bigcone Douglas-fir was sampled is typical of the species habitat. Precipitation falls mostly in winter, seldom in summer. Annual precipitation ranges from 356 to 1016 mm. On windward slopes, precipitation increases with elevation. For example, in the San Bernardino Mountains annual precipitation at Santa Ana River Powerhouse number 3 (elev. 843 m) is 378 mm, at Mill Creek intake (elev. 1512 m) 654 mm, and at Running Springs (elev. 1819 m) 931 mm (U. S. Weather Bureau, 1964).

Temperatures throughout the study area are moderate and warm. Mean annual temperature is about 14°C. Extreme high and low temperatures are 41°C and −12°C. Even winter months can be warm (Sinclair et al., 1953), and in some years at least one of the winter months can be warmer than May or June (Hellmers, 1959).

The 16 sample stands represented the species over a wide range of physiographic conditions. Elevations ranged from 732 m to 1830 m. Slopes varied from 1 to 93 percent, and numerous aspects were represented.

Various soil characteristics such as color, depth, texture, and parent material were physically noted for each stand and then referred to a geology text for southern California (Jahns, 1954), the Geologic Map of California (Calif. Dept. Natur. Resour., 1955; 1965; 1967), and to soil series. California soil series are identified by the California Cooperative Soil-Vegetation Survey and the National Cooperative Soil Survey.

In this report, relationships are presented individually for bigcone Douglas-fir, canyon live oak, and "associated" species. "Associated" collectively means all tree species except bigcone Douglas-fir and canyon

live oak. We further subdivided the tree category into various diameter classes and recorded the number of stands in each.

Results

Elevational Gradients. Trees accompanying bigcone Douglas-fir were divided about evenly between conifers and hardwoods. As associates, each occupied a fairly distinct elevational range (fig. 2).

Where present, bigcone Douglas-fir trees form small, rather dense groves or exist as scattered individuals. Occasionally, the lower slopes of entire hillsides abound with this species, but more commonly stand size is about 0.1 ha.

Where bigcone Douglas-fir regeneration was found, seedling density ranged from 138 to 1027 per ha, with an average of 326. Advance repro-

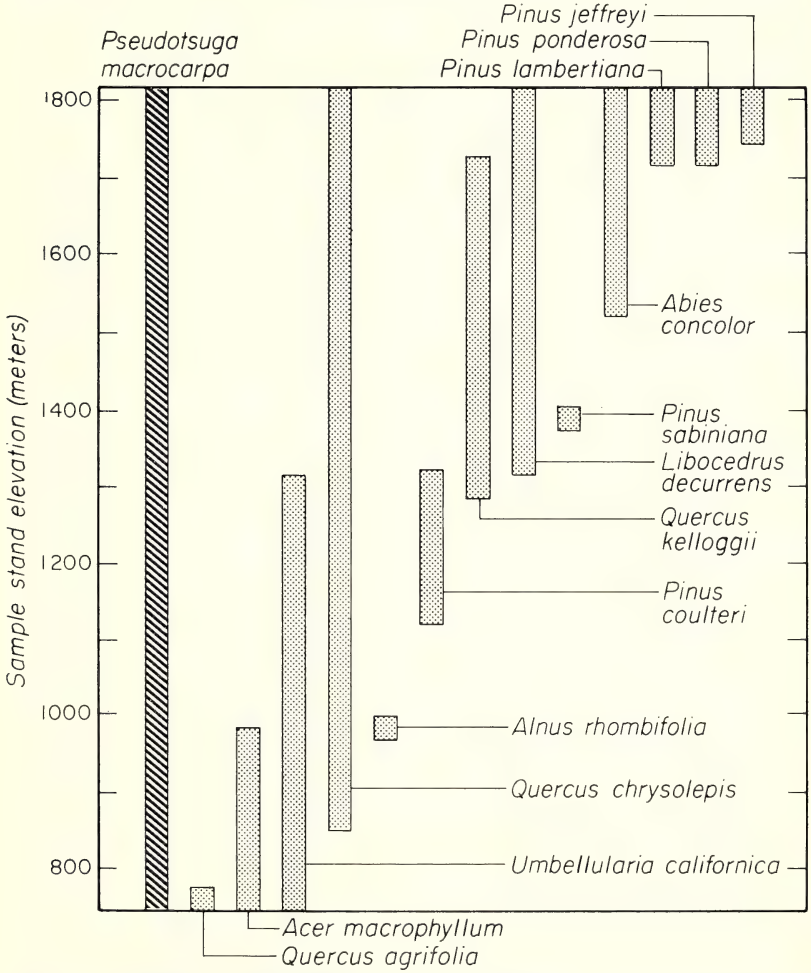

Fig. 2. Elevational distribution of bigcone Douglas-fir, canyon live oak, and other tree associates within sampled bigcone Douglas-fir range.

duction had a near-similar mean and range in density. The tree category ranged from 2.8 to 137.2 cm d.b.h. Its density varied from 20 to 662 and averaged 267 trees per ha. Examination of these values indicated that bigcone Douglas-fir seedlings, advance reproduction, and trees were evenly distributed along the elevational gradient.

Of the 16 stands, the best-represented diameter class for bigcone Douglas-fir was the largest class, and the poorest was the regeneration class (Table 1). Furthermore, each stand included at least two diameter classes, several five; the average was four.

The basal area of bigcone Douglas-fir trees exceeding 2.5 cm d.b.h. ranged from about 5 m^2 per ha to about 253 m^2. The number of stems was inversely related to basal area: the smallest number of stems occurred in the largest diameter classes, which in turn had the highest basal areas. This was particularly true of stands with trees 50.9 cm in diameter and larger.

Where canyon live oak regeneration was present, its density ranged from 20 to 1570, averaging 365 seedlings per ha. Canyon live oak regeneration was found in five of the six stands having bigcone Douglas-fir regeneration. Canyon live oak advance reproduction averaged 345 plants per ha, and occurred in 7 of the 8 stands having bigcone Douglas-fir advance reproduction. The density of canyon live oak trees in the diameter range of 2.8 to 91.4 cm ranged from 20 to 1423 with an average of 395 plants per ha. Further examination showed that canyon live oak seedlings, advance reproduction, and trees were evenly distributed along the elevational gradient.

In the 16 stands, canyon live oak was best represented in the 4 smallest diameter classes and poorly represented in the 3 largest classes (Table 2). This representation is almost the exact opposite of bigcone Douglas-fir.

Each stand was analyzed further to ascertain the number of diameter classes in each. They ranged from none to six. The average was four—the same as for bigcone Douglas-fir.

Basal area of canyon live oak ranged from 1 to 124 m^2 per ha. It exceeded the basal area of bigcone Douglas-fir through the 2.8- to 50.8-cm

Table 1. Diameter Class Representations in Samples from Sixteen Stands of Bigcone Douglas-fir.

Diameter class (cm)	Number of stands where diameter class is present
Regeneration	6
Advance reproduction	8
2.8 – 10.2	9
10.3 – 30.5	11
30.6 – 50.8	9
50.9 – 76.2	7
76.3+	13

TABLE 2. DIAMETER CLASS REPRESENTATIONS IN SAMPLES FROM SIXTEEN STANDS OF CANYON LIVE OAK.

Diameter class (cm)	Number of stands where diameter class is present
Regeneration	12
Advance reproduction	13
2.8 – 10.2	10
10.3 – 30.5	13
30.6 – 50.8	5
50.9 – 76.2	6
76.3+	5

diameter class, equalled it in the 51.1- to 76.2-cm class, and was only one-third of it in the largest diameter class. Canyon live oak basal area was less than bigcone Douglas-fir in 11 of the 15 stands where both grew. The magnitude of difference was over two to one in favor of bigcone Douglas-fir. A paired "t" test (Snedecor, 1956) of the two species indicated a significant difference in basal areas at the 1 percent level of probability.

Regeneration of associated species was noted in seven stands. Of these species, *Quercus kelloggii* was most successful, regenerating in four stands; *Umbellularia californica* was present in three. Where present, regeneration of associated species averaged 119 plants per ha. For advance regeneration, which was observed in ten stands, *Umbellularia californica* grew in five stands and *Libocedrus decurrens* in three stands. Average density for advance reproduction was about 168 plants per ha and rarely included more than three species.

Tree density of associated species ranged from 49 to 850 stems per ha, but densities of individual species ranged from 49 to 326 with an average of 109.

Tree associates of bigcone Douglas-fir were not as widespread as it in terms of elevation. Presence of each species was calculated as a percentage of the 16 sampled stands (Table 3).

Aggregate basal area of the associated species ranged from 1 to 40 m^2 per ha. Average values were intermediate between those of bigcone Douglas-fir and canyon live oak up to 50.8 cm in diameter, and less than either species above this diameter. Placement along the elevational gradient yielded no meaningful trends for basal area or density.

High and low basal area values for bigcone Douglas-fir, canyon live oak, and associated species in each diameter class were randomly dispersed along the gradient.

Basal areas indicate not only relative diameters but also the extent that a given area is occupied by trees. For all tree species combined, stand basal area ranged from 40 to 293 m^2 per ha, averaging 126 m^2.

Members of the woody shrub genera *Arctostaphylos, Ceanothus, Rhamnus, Ribes,* and *Rhus* are almost totally lacking beneath the big-

TABLE 3. PRESENCE OF TREE SPECIES ASSOCIATED WITH BIGCONE DOUGLAS-FIR. Presence is expressed as a percent of 16 stands in which the species occurred.

Species	Percent	Species	Percent
Quercus chrysolepis	94	*Pinus lambertiana*	12
Umbellularia californica	44	*Pinus ponderosa*	12
Libocedrus decurrens	44	*Quercus agrifolia*	6
Quercus kelloggii	38	*Alnus rhombifolia*	6
Acer macrophyllum	25	*Pinus sabiniana*	6
Abies concolor	25	*Pinus jeffreyi*	6
Pinus coulteri	19		

cone Douglas-fir stands. But because these shrubs are often located on the fringes of the sample stands, many seeds undoubtedly are in the upper soil (Quick, 1956).

Slope and Aspect Gradients. The 16 stands were arranged along slope and aspect gradients by plotting density and basal area. No trends materialized for bigcone Douglas-fir, canyon live oak, or associated species.

The interaction of aspect and elevation, however, seemed to govern the occurrence of bigcone Douglas-fir. At lower elevations, this species grows near streams in moist, shaded canyons and draws, where aspects are mostly north and east. As elevation increases from 1350 to 1700 m, aspects broaden to include more south- and southeast-facing slopes. At these higher elevations, benches, sloping hillsides, and ridges often are clothed with this species. At bigcone Douglas-fir's highest elevational zone (over 1700 m), it is found on warmer south and west aspects without regard to canyons, streams, and draws.

Available Moisture Gradient. Numerous factors were considered in establishing the moisture gradient. In order of magnitude they were: (1) presence of a permanent stream; (2) presence of an ephemeral stream; (3) degree of moisture stress in trees as noted by Griffin (1967), Waring (1969), and Wilson and Vogl (1965); and (4) aspect, slope, and elevation. On the basis of these factors, four stands were rated as xeric, three as moderately xeric, three as moderately mesic, and six as mesic. Among these habitats, density and basal area by species were then compared.

Bigcone Douglas-fir and canyon live oak regeneration and advance reproduction were present in all habitats. Both species in both size classes were more dense, however, in stands rated as xeric or moderately xeric. Bigcone Douglas-fir and canyon live oak trees were well represented in all habitats. No trends in density or basal area were identified.

Soil Depth and Latitudinal Gradients. Soil parent materials generally belonged to two classes—granitics and metasedimentaries (sandstone and schist). Of the 16 sampled stands, four grew on metasedimentary parent materials, ten on granitics, and two in contact zones where the parent material was primarily granitic. Tentative soil series on meta-

sedimentary material were Laughlin and Friant; in contact zones, Oak Glen; and on granitics, Tollhouse, Cieneba, Crouch, and two others that resembled Tish Tang and Neuns.

In general, soils showed a broad range of depth and development. Some were shallow and poorly developed, others were deep and better developed. Nearly all, however, were coarse textured and well drained.

Arraying density and basal area by species and size classes along soil depth and latitudinal gradients showed no trends. Within the study area, changes in latitude and soils scarcely affect the stability and site preference of bigcone Douglas-fir. The possibility exists that added moisture and cooler temperatures resulting from fog in the Santa Ana and Agua Tibia Mountains might benefit bigcone Douglas-fir. But since no differences were found along the latitudinal gradient, fog apparently is not a meaningful factor.

Discussion

Evidence is strong that the sample stands have been free of major disturbance for many years. That both bigcone Douglas-fir and canyon live oak average four diameter classes per stand and that the usually abundant woody shrub species are absent support this thought. Thus, regeneration, advance reproduction, and tree data, as presented, are representative of stand development in an undisturbed state.

Although bigcone Douglas-fir and canyon live oak associate closely, similarities and differences exist among seedlings, advance reproduction, and trees. Average densities of seedlings and advance reproduction of both species are similar. When combined for both species, average density is 1324 plants per ha. For trees smaller than 30.5 cm in diameter, canyon live oak is more dense; for those above 30.5 cm, bigcone Douglas-fir density rates highest. A generally similar and statistically significant relationship between the two species also holds for basal area.

Canyon live oak's poorer representation in the larger diameter classes probably results from a combination of environmental and genetic factors. Because canyon live oak sprouts from the root crown after fire or other damage, it often produces clones. With fire commonplace throughout the mountains of southern California (Wilson and Vogl, 1965; Wright, 1966; Vogl and Miller, 1968), most of the hardwoods are clonal and have three to five stems per clone. Individual trees within these clones seldom reach 76.2 cm in diameter.

Another strong relationship is the ability of bigcone Douglas-fir regeneration and advance reproduction to grow under dense stands of canyon live oak or of both species. Where basal area levels are high, however, regeneration of bigcone Douglas-fir generally is absent.

In addition to canyon live oak, other species of trees also reside within the sampled range of bigcone Douglas-fir. The degree of occurrence of individual species (presence) is low, however, and ranges from 6 to 44

percent. Most often, these tree associates and their regeneration are less numerous than bigcone Douglas-fir and canyon live oak, and their overall basal area is much lower. While an integral part of most stands, they do not appear to threaten domination of any stand.

Taken together, all factors studied demonstrate the existence of an ecological unit, the bigcone Douglas-fir–canyon live oak community. This community in the forests of southern California is distinguished principally by its remarkable ecological stability. Several characteristics emphasize this stability:

1. Both species are long-lived and relatively large.
2. Both species have only moderate reproductive potential and rather limited seed dispersal. Seed crops are infrequent for bigcone Douglas-fir (Gause, 1966). While seed crops are more frequent for canyon live oak, a high proportion of acorns often are infertile.
3. Early seedling growth of both species is slow, enabling large numbers of seedlings to accumulate.
4. Seedlings show little seedbed preference but do best under an overstory or on the shaded overstory fringes.
5. Both species grow rather slowly, although bigcone Douglas-fir accelerates growth after reaching above the oak overstory.
6. Both species possess strong survival mechanisms, chiefly sprouting ability. This characteristic is unusual for a North American conifer.

Because of this stability, the areal extent of the bigcone Douglas-fir–canyon live oak community will change little, if any. If changes do take place, they will occur within the community. The two principal species, having similar ecological characteristics, are probably in dynamic equilibrium. Shifts in this equilibrium result from major disturbances, primarily fire.

By knowing the autecology of the species in the community, and by carefully observing stand structure and species composition of many stands, a trained observer can put together a developmental sequence for undisturbed and disturbed stands.

With continued exclusion of fire, bigcone Douglas-fir seedlings beneath the canyon live oak canopy eventually grow through it and dominate. Fir seedlings on the fringes of undisturbed oak stands also become dominant. Therefore, with the absence of fire, fir trees eventually replace the oaks and dominate the community. This is a slow steady process, however, and results in only minor changes in stand composition and structure.

When the community burns, all but the largest bigcone Douglas-firs are killed. Large trees live by resprouting along the boles, but their ability to produce seed is impaired for years. Thus, after fire, bigcone Douglas-fir in the community is limited to large sizes. Most burned canyon live oaks promptly sprout from root crowns. So do oak seedlings and advance reproduction on the forest floor. Thus presence of canyon live oak in the community is relegated to the smaller size classes.

With or without fire, additional area lost or gained by the community is likely to be small.

The overall pattern of the bigcone Douglas-fir–canyon live oak community is that of a stable, self-perpetuating, somewhat exclusive community, with tendencies toward the climax or even postclimax successional stage. Weaver and Clements (1938) implied that the postclimax community is usually a relict community as well. Such a community would exist in an area where the local climate, topography, or soil would compensate for the aridity of modern, as contrasted to Miocene, times. Vegetation in gorges, canyons, and "long and steep slope exposures" qualified under the Weaver and Clements definition of postclimax. Certainly these conditions typify the habitat of the present-day bigcone Douglas-fir–canyon live oak community. Indeed, Cooper (1922) called the entire broad sclerophyll forest, of which this community is a part, postclimax.

Axelrod (1937) and Mason (1940) found evidence of a progenitor of bigcone Douglas-fir in both the Pliocene and Pleistocene epochs. Fossil specimens similar to *Quercus chrysolepis* and *Q. agrifolia, Pinus coulteri* and *P. sabiniana,* and *Sequoia* spp. of today also were found in association. That the bigcone Douglas-fir–canyon live oak community is a relict community is likely.

An almost complete lack of correlation exists between this community and the variables quantified in this study. Edaphic and physiographic variables were particularly unimportant—at least at the magnitude of sampling used. Most of the many combinations of slope, aspect, soil, and elevation examined similarly support the bigcone Douglas-fir–canyon live oak community. This suggests that, as individual factors vary among the stands, they complement each other and, together, provide environments that are nearly alike biologically. Thus the community seems to be narrowly endemic, occupying a specific habitat in the canyons and on the slopes of mountainous southern California.

In California's Santa Ana mountains, Bolton and Vogl (1969) found that "bigcone Douglas-fir will continue to occupy the same relative position to other vegetation types in the future, and that only by rapid environmental changes can it be reduced or increased from its present status". This work supports their finding and extends it to most of the natural range of the species.

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MEXICAN SPECIES OF ABUTILON SECT. ARMATA (MALVACEAE), INCLUDING DESCRIPTIONS OF THREE NEW SPECIES

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Abutilon Mill. sect. *Armata* Presl is a natural group. Critical revision of the entire genus, including typification and evaluation of the approximately 25 infrageneric groups that have been named, may lead to the conclusion that this taxon should have another name and/or different rank; the group is thus accepted only provisionally as sect. *Armata*.

Characteristic features of this taxon include robust growth habit,

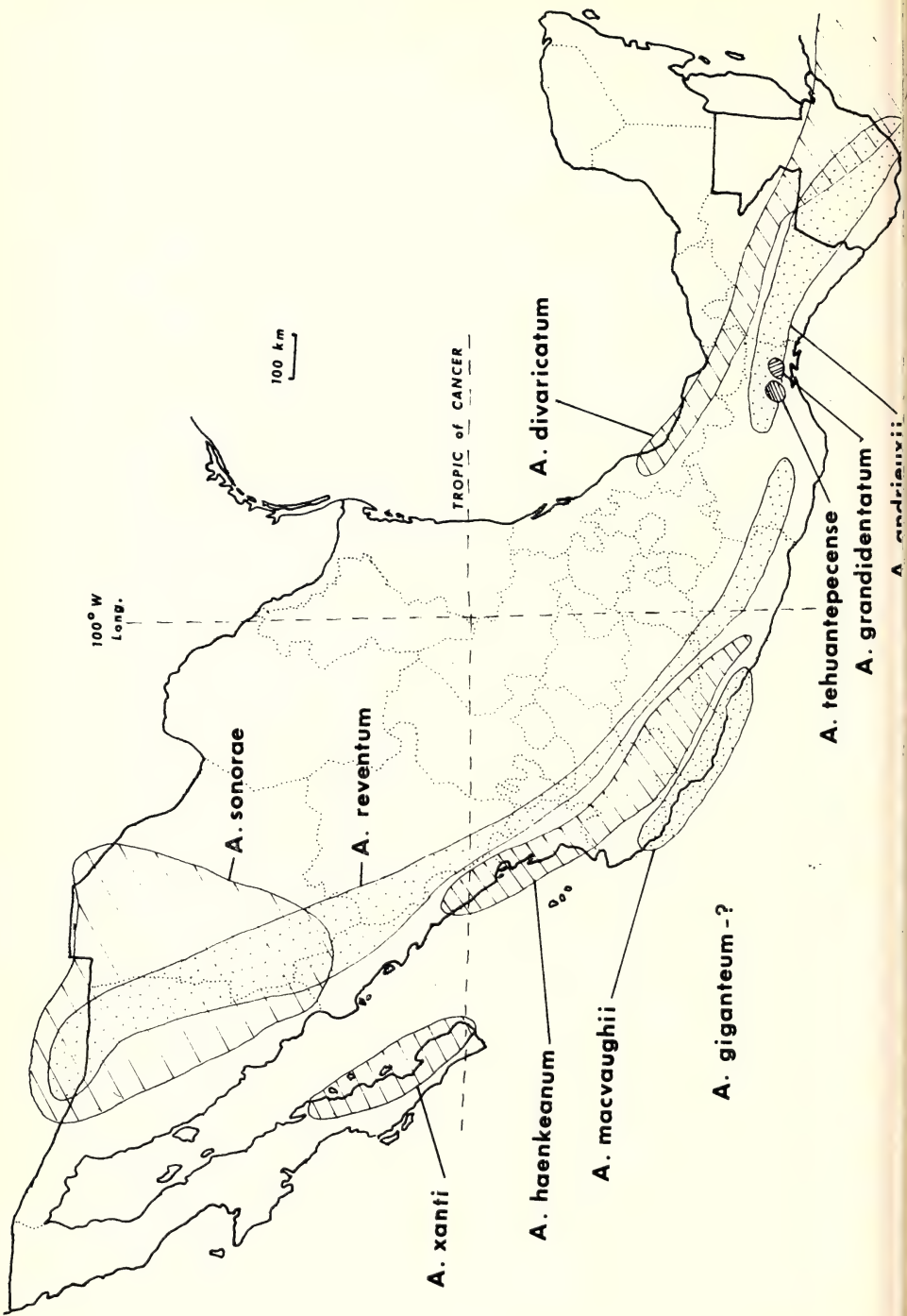
inflorescences of ample terminal panicles, reflexed petals, and distinctive floral bracts. Not all of the species have all of these characteristics, but the group nevertheless is distinct morphologically from the remainder of the genus. In addition to the Mexican species that are the subject of this paper, the group includes species from Central America [*A. cymosum* Triana & Planch.], the Caribbean [*A. elatum* (Macf.) Griseb.], and South America [e.g., *A. stenopetalum* Garcke, *A. thyrsodendron* Griseb., *A. oxypetalum* Planch. & Lind., *A reflexum* (Juss. ex Cav.) Sweet]. The Australasian *Abutilon auritum* (Wall. ex Link) Sweet is reported to reach Mexico and other parts of the neotropics as an adventive, but it seems probable that these reports are based at least in part on misidentified specimens of the very similar *A. elatum, A. andrieuxii* Hemsl., and *A. haenkeanum* Presl. The relation between these Old and New World species deserves detailed investigation.

Examination of some recent collections of *Abutilon* from Mexico led to recognition of three new species that belong to this section; these are described below.

In reviewing the section, it became apparent that Kearney (1955), in his key to North American species of *Abutilon* (the best available key to these plants), misunderstood the occurrence of reflexed petals (as did Baker, 1893) and the development of stipules, two important characters in this group. I have therefore prepared a key to the ten species of *Abutilon* sect. *Armata* that occur in Mexico and supplemented this with distributional and other data on these species. All of these species are confined to Mexico except *A. andrieuxii, A. divaricatum* Turcz., and *A. giganteum* (Jacq.) Sweet, which extend southward, the last-named occuring principally in northern South America, and *A. sonorae* A. Gray and *A. reventum* S. Wats., both of which may also be found to the north in southwestern United States (see fig. 1).

ABUTILON sect. ARMATA Presl, Rel. Haenk. 2:114. 1835. Lectotype (here designated): *Abutilon haenkeanum* Presl, Rel. Haenk. 2:115. 1835.

Plants robust, sometimes arborescent, often large shrubs or sub-shrubs, sometimes herbaceous perennials, but generally of vigorous growth, commonly 2 m or more high. Leaves long-petiolate, deeply cordate, subentire to dentate, often acuminate, simple and ovate or somewhat trilobed. Stipules variable: usually early caducous, sometimes large and conspicuous, toothed or laciniate and/or auriculate-clasping, sometimes narrowly subulate. Inflorescence an ample terminal panicle, usually of such proportions as to be difficult to represent adequately in a dried specimen. Characteristic floral bracts in pairs, subtending individual flowers as a pseudo-involucel, often enclosing the buds, the bracts early-caducous, often connate along their dorsal margin and sometimes apically dentate or laciniate; they are interpreted as modified stipules. Flowers usually small, the petals often reflexed, white, yellow, orange, or (in two species) violet or purple. Fruits ca 1 cm long (to 2 cm in *A. divaricatum*); meri-


100 km
TROPIC of CANCER
100° W Long.
A. divaricatum
A. sonorae
A. reventum
A. tehuantepecense
A. grandidentatum
A. xanti
A. haenkeanum
A. macvaughii
A. giganteum-?

carps 6–10 (12–15 in *A. giganteum*), usually rounded or acute and short-spined apically, sometimes acuminate.

In proposing *Abutilon* sect. *Armata,* Presl included eight species. In order to clarify Presl's concept, I choose *A. haenkeanum* as lectotype. In addition, I exclude four of the eight species that he included: *A. triquetrum* (L.) Presl, *A. ramosissimum* Presl [both of which are synonymous with *A. trisulcatum* (Jacq.) Ulbr.], and two Peruvian species, *A. calycinum* Presl and *A. vitifolium* (Cav.) Presl. The last-named is the type species of the genus *Corynabutilon* (K. Schum.) Kearn.

Key to Mexican species of *Abutilon* sect. *Armata* Presl

a. Petals violet or purple throughout, reflexed; calyx 10–15 mm long; stems viscid; staminal column pubescent (Oaxaca).
  b. Petals purple, wholly glabrous; calyx 12–15 mm long; filaments 3–5 mm long; leaves coarsely dentate, often weakly trilobed; stems with long, simple hairs (1–2 mm long) in addition to glandular hairs. . . . . 1. *A. grandidentatum* (fig. 2)
  bb. Petals violet, stellate-pubscent externally on proximal third; calyx 10–12 mm long; filaments 2.0–2.5 mm long; leaves denticulate, unlobed (?); stems lacking long, non-glandular hairs. 2. *A. tehuantepecense*

aa. Petals white, buff, yellow, or orange, sometimes with dark basal spot, reflexed or not; calyx 4–11 mm long; stems usually not viscid; staminal column glabrous or pubescent.
  c. Pedicels stout (1.5–2.0 mm diam.); petals markedly reflexed, with basal spot; staminal column glabrous, 5–9 mm long; filaments 4–5 mm long; mericarps 12–15 (Mexico?, South America). 3. *A. giganteum* (fig. 3, A–C)
  cc. Pedicels slender (up to 1 mm diam.); petals reflexed or not; staminal column glabrous or pubescent, 2–6 mm long; filaments 1–4 mm long; mericarps 8–12.
    d. Simple hairs of stem and petioles dense, 1–2 mm long, somewhat retrorse; mericarps 12–20 mm long, strongly keeled dorsally; calyx divided almost to the base, the lobes narrow and fully reflexed in fruit; petals yellowish or buff with basal spot, stellate-pubescent externally at base (Mexico to Panama). 4. *A. divaricatum* (fig. 3, D–G)
    dd. Simple hairs on stem and petioles sparse or lacking (or present in *A. sonorae* and > 2 mm long and patent); mericarps 8–12 mm long; calyx ½–⅔-divided, the lobes not reflexed in fruit; petals usually without basal spot.
      e. Petals yellow or white, glabrous; staminal column glabrous; stipules narrow and inconspicuous.
        f. Petals yellow, 9–13 mm long; mericarps obtuse; stems often dark-pigmented, sparsely and minutely viscid-pubescent and stellate-pubescent to glabrate (Oaxaca to Arizona). 5. *A. reventum* (fig. 4, A–B)

ff. Petals yellow to white, 5–9 mm long; mericarps apiculate or acuminate; stems often densely pubescent but not viscid.

g. Stems and petioles with long, simple hairs 2–3(–4) mm long (these sometimes lacking in inflorescence); calyx 4–5 mm long; petals 5–6 mm long, yellowish (Guerrero to Arizona). . . . . 6. *A. sonorae* (fig. 4, C–F)

gg. Stems and petioles velvety-tomentose, lacking long, simple hairs; calyx 6–12 mm long; petals 7–9 mm long, whitish, sometimes somewhat reflexed (Baja California). 7. *A. xanti* (fig. 4, G–H)

ee. Petals yellow or orange, often with minute external pubescence; staminal column stellate-pubescent at least at base; stipules broad and prominent, auriculate-clasping (but caducous).

h. Petals yellow, 18–20 mm long, not reflexed, externally stellate-pubescent at base; calyx 8–10 mm long; filaments 3–4 mm long; mericarps apically acute (coastal Jalisco and Guerrero). . . . 8. *A. macvaughii* (fig. 5, F–G)

hh. Petals orange, 8–12 mm long, reflexed, often with scattered multicellular hairs externally at least on margin; calyx 4–10 mm long; filaments 1.0–1.5 mm long; mericarps apically obtuse or acute.

i. Calyx 4–7 mm long (< half length of mericarps); mericarps short-puberulent, relatively blunt or acute apically (Oaxaca and Chiapas, Guatemala, and El Salvador). 9. *A. andrieuxii* (fig. 5, A–D)

ii. Calyx 6–10 mm long (> half length of mericarps); mericarps long-hirsute, acuminate (Guerrero to Sinaloa). 10. *A. haenkeanum* (fig. 5, E).

1. **Abutilon grandidentatum** Fryx., sp. nov. sectionis *Armatae* (fig. 2). Arbor parva vel frutex grandis, ramunculis pilis brevibus (< 0.5 mm) glanduliferis obtectis, interdum pilis longis (> 1 mm) eglanduliferis immixtis, demum glabrescentibus. Folia profunde cordata, late ovata, interdum leviter 3-lobata, acuminata, grosse dentata (dentibus 2–6 mm longis, 4–6 mm latis), palmatim 9-nervata, nervis pallidis, usque ad 10 cm longa, 9 cm lata, utrinque dense et molliter pubescentes, pubescentiis stellatis et albidis, plus minusve discoloria saltem juventute. Petioli usque ad 6 cm longi (quam lamina brevior), pubescentiis caulis similis. Stipulae 7–15 mm longae, angustae (2 mm latae) et lanceolatae vel latiores (5–6 mm latae) et ovatae, interdum paribus stipularum connatis in marginibus dorsalibus organum singulum formantia, membrancea, pubescentes, manifestae sed maturae caducae; paria stipularum infra quoque alabastrum in inflorescentia pseudo-involucellum formantia. Flores 2–3 cm diam., interdum in axillis solitarii sed plerumque in paniculis terminalibus congestis. Pedicelli 2–10 mm longi, glanduloso-

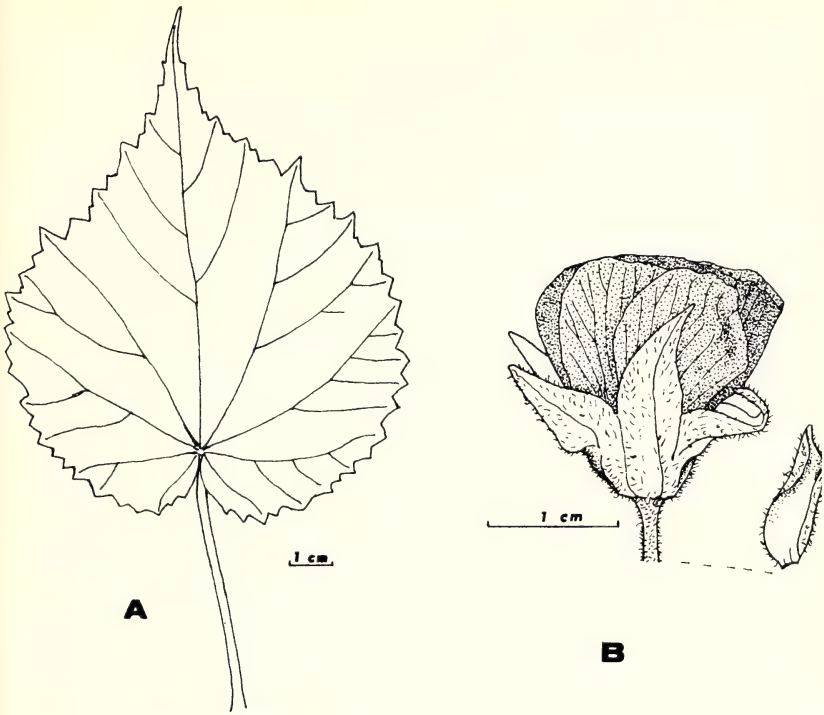


FIG. 2. *Abutilon grandidentatum* (*MacDougall H143*). A, leaf; B, flower and floral bract.

pubescentes, interdum pilis longis eglandulosis adjectis. Calyces 12–15 mm longi, utrinque dense pubescentes, pilis stellatis et pilis (longis) simplicibus instructis, saepe ad basim brunneoli, plus quam semi-divisi, lobis 1-nervatis, ad basim 4–5 mm latis, 8–10 mm longis. Petala purpurea, reflexa ut videtur, 10–15 mm longa, 8–15 mm lata, glabra; unguis 3-4 mm lata. Columna staminalis 5 mm longa, infra semi-globosa (3–4 mm diam.), supra in columna 1 mm diam. angustata, pallida, stellato-pubescentes praesertim infra; filamenta numerosa, ex apice columnae plus minusve erecta, 3–4 mm longa, pallida, glabra; antherae armeniacae; pollen armeniacum, globulosum, spinosum. Styli stamina excedentes demum, ca 8, glabri, purpurascentes; stigmata capitata, atropurpurea. Fructus 8–10 mm longi, stellato-pubescentes praesertim secus suturas, pilis multicellularis glandularis in pariete dorsali; mericarpia ad apicem acuta, dehiscentia, 1–3-seminalis.

TYPE: Mexico, Oaxaca, Cerro Guiengola near Tehuantepec, elev. 500 ft, compact shrub to ca 5 ft, flowers rose-purple, in sun, 11 Dec 1971, *T. MacDougall H143*. Holotype: NY; isotypes: F, pf. PARATYPES: Mexico, Oaxaca, Jalapa [near Tehuantepec], Cerro Calderona, elev. 100–2000 ft, small tree with purple-red flowers, in sun, 18 Feb 1972,

T. MacDougall H270 (NY, pf); Ocotita, near Tehuantepec, elev. 500 ft, tree with purple flowers, in sun, 8 May 1972, *T. MacDougall H442* (NY, pf).

DISTRIBUTION: Known only from the specimens cited above, from the vicinity of Tehuantepec, Oaxaca, at low elevation.

This species is distinctive in its coarsely dentate leaves (fig. 2, A), its purple corolla, and its relatively large calyx (fig. 2, B). It is surprising that this species has not been recognized before, since it is a robust shrub or small tree with relatively showy flowers. The restricted distribution of the species is probably the reason this is so.

2. **Abutilon tehuantepecense** Fryx., sp. nov. sectionis *Armatae*. Arbor staturae ignotae sed probabiliter parva. Ramunculi juventute minute et dense glanduloso-puberuli, demum glabrati et aliquantum striati vel angulati. Folia valde discoloria, cordata, ovata, acuta vel acuminata, palmatim 7–9-nervata, leniter denticulata, infra minute pannosa; (folia bene evoluta destituta). Petioli minute stellato-puberuli, quam lamina dimidio longiori. Stipulae 5–9 mm longae, 2–4 mm latae, lanceolatae vel interdum (in inflorescentia) paribus stipularum connatis secus margines dorsales alabastrum includentibus, glanduloso-pubescentes, maturae caducae. Inflorescentia paniculata ut videtur. Flores 15–20 mm diam. Pedicelli 5–12 mm longi, glanduloso-puberuli. Calyces 10–12 mm longi, in alabastro plicati, dense albo-tomentosi, plus quam semi-divisi, lobis ad basim 3–4 mm latis, 7–9 mm longis, triangularis, 1-nervatis, demum ad basim gibbosescens. Petala lavandulacea (vel color in sicco destructus), reflexa, 10–11 mm longa, 5–7 mm lata, unguibus 2–3 mm latis, intus glabra praeter dense coacta in marginibus unquium, extus dense stellato-pubescentia in tertia parte proximali et glabra in parte distali. Columna staminalis dense stellato-pubescens ubique, ad basim 2.5–3.0 mm diam. gradatim decrescens sursum ad 1.0 mm diam., superne purpurascens; filamenta ex tertia parte distali columnae exorientia, vix purpurascentia vel atropurpurea, glabra, 2.0–2.5 mm longa, plerumque reflexa; antherae luteolae, $<$ 1 mm longae; pollen luteum, globulosum, spinosum. Styli ca 6, pallidi, androecium vix aequantes; stigmata capitata, viridi-purpurea vel atropurpurea. Fructus 1 cm longi, calycem subaequantes, stellato-pubescentes; mericarpia ca 6, ad apicem acuminata, calcari 1 mm longo, dehiscentia, pluri-seminalis ut videtur.

TYPE: Mexico, Oaxaca, Tehuantepec, Cerro de las Animas, tree with pale violet flowers, in sun, 27 Dec 1971, *T. MacDougall H166*. Holotype: NY; isotypes: F, pf. PARATYPE: Mexico, Oaxaca, San Bartolo Yautepec, Puerto San Bartolo, elev. 2500 ft, tree with purple flowers, orange stamens, in sun, 2 Feb 1972, *T. MacDougall H229* (NY, F, pf.)

DISTRIBUTION: Known only from the specimens cited above, from near and to the west of Tehuantepec, Oaxaca, evidently at somewhat higher elevation than the preceding species.

This species is distinctive in its arborescent habit and violet flowers.

Like the preceding species it has probably escaped discovery until now because of a restricted distribution.

3. ABUTILON GIGANTEUM (Jacq.) Sweet, Hort. Brit. ed. I. 1:53. 1826.—*Sida gigantea* Jacq. TYPE: Hort. Schoenbr. *t. 141!* (from Venezuela).

Abutilon mexicanum Presl, Rel. Haenk. 2:115. 1835. TYPE: In terris mexicanus occidentalibus, *Haenke s.n.* Holotype: PR!

Abutilon pseudogiganteum Steyerm., Fieldiana, Bot. 28:362. 1952. TYPE: Venezuela; Anzoátegui; between San José and Cucutá, *Steyermark 61519*. Holotype: F!.

DISTRIBUTION: Northern South America; although freely reported from Central America to southern Mexico (largely on the basis of misidentified specimens of *A. divaricatum*), it is known to me from Mexico only by Haenke's specimen, the type of *A. mexicanum*.

This species is distinctive for its reflexed petals with a basal spot on each, its long staminal column (fig. 3, A), its relatively stout pedicels (1.5–2.0 mm diam.), and its more numerous (12–15) mericarps (fig. 3, B). It has been confused with *A. divaricatum* and with *A. elatum* [e.g., by Standley (1923, 1937) and Standley and Steyermark (1949)] but is clearly distinct from both. The preceding key (and fig. 3) distinguish *A. giganteum* and *A. divaricatum*; the Caribbean *A. elatum* differs from them in petal color and in having smaller mericarps, smaller stipules, and velvety indumentum. *Abutilon elatum* is closely allied to *A. andrieuxii* and *A. haenkeanum*.

REPRESENTATIVE SPECIMENS: Mexico, *Haenke s.n.* (PR). Venezuela, *Fernandez 436* (F), *Montaldo 3622* (F), *Krapovickas 15568* (CTES, MO, pf). Colombia, *Smith 732* (F, MICH, MO, TEX), *Killip et al. 38224* (F), *Haught 2410* (F), *Cuatrecasas and Perez Arbeláez 6569* (F). Peru, *Ferryra 7739* (F), *Klug 3887, 4370* (F, MO).

4. ABUTILON DIVARICATUM Turcz., Bull. Soc. Imp. Naturalistes Moscou 31:204. 1858. LECTOTYPE (here designated): Veracruz, Mirador, *Galeotti 4071*. Hololectotype: presumably at KW, not seen; isolectotype: BR!, G, as photo F!.

Abutilon chiriquinum A. Robyns, Ann. Missouri Bot. Gard. 52:574. 1966. TYPE: Panama, Prov. Chiriqui, vicinity of El Boquete, *Bro. Maurice 705*. Holotype: US!

DISTRIBUTION: Veracruz and Chiapas, through Central America as far south as Panama, mostly from elevations of 1200–2300 m but occasionally at lower elevations.

This species is distinctive in its narrow calyx lobes that are fully reflexed in fruit (fig. 3, D–E), in its large, prominently keeled mericarps (fig. 3, E), and in its dense, somewhat retrorse stem pubescence (fig. 3, F).

This species has been poorly understood for several reasons. Turczaninow cited two collections from Veracruz (*Galeotti 4071* and *Linden*

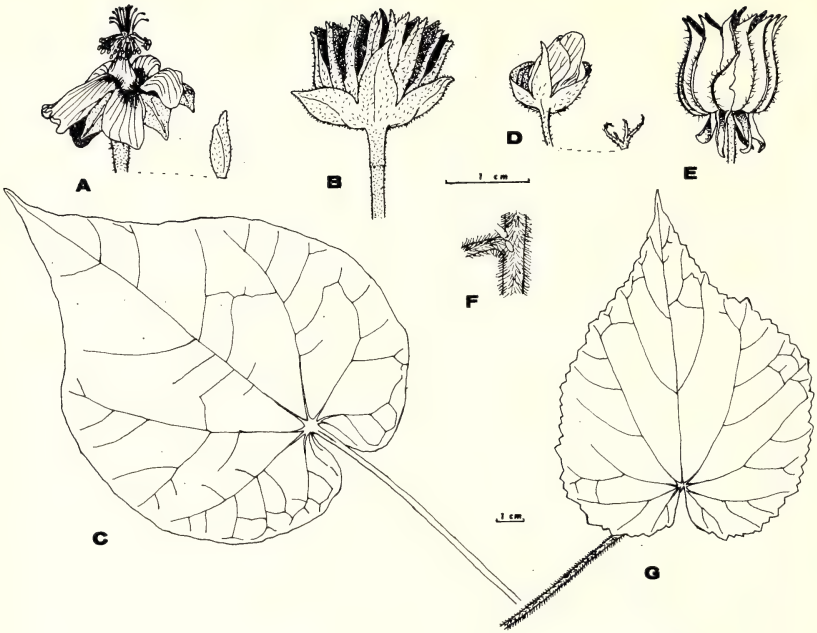


FIG. 3. A–C, *Abutilon giganteum*. A. flower and floral bract (*Haught 2410*); B, fruit (*Cuatrecasas and Perez Abeláez 6569*); C, leaf (*Killip et al. 38224*). D–G, *Abutilon divaricatum*. D, bud and floral bract (*Rosas 1468*); E, fruit (*Steyermark 34393*); F, stem and petiole, illustrating nature of vestiture (*Rosas 1468*); G, leaf (*Molina et al. 15969*).

1378) and one from Ecuador (*Jameson 605*). These three collections represent two species. A duplicate (presumably at B or BR) of the Jameson specimen was later cited as a syntype of *Abutilon cordatum* Garcke & Schum. (non Rafin.), the name by which the plant from Peru and Ecuador is now known (e.g., Baker, 1893; Macbride, 1956).

Baker (1893) recognized the distinctiveness of *A. divaricatum* (having examined duplicates of the Jameson and Linden specimens) and cited *Jameson 605* for *A. cordatum* and *Linden 1378, Galeotti 4071,* and *Borgeau 1740* (all presumably at BM) for *A. divaricatum;* he failed to note that the Jameson collection was cited in the protologues of both names. This was noted by Garcke (1893), who had also examined the Jameson collection (but not the others) and who observed that its dispermous condition was in contradiction to Turczaninow's description of *A. divaricatum*. However, Garcke (who was followed by Kearney, 1958) failed to conclude that two species were involved, as Baker had done, even though Schumann (1891, p. 398), with whom Garcke co-authored *A. cordatum,* clearly implied that Turczaninow's name referred to a mixture of two species. Garcke therefore accepted the older name *A. divaricatum* (and considered *A. cordatum* superfluous) and applied it to

the South American plant, since he had studied only the Jameson specimen and none of the Veracruz material. Kearney (1958) accepted this view and, in his treatment of North American species of *Abutilon* (1955), omitted reference to *A. divaricatum,* evidently confusing this plant with *A. giganteum,* probably because Standley (1923, 1937) and Standley and Steyermark (1949) had earlier confused these two species, citing specimens of the former under the latter name.

It seems best to restrict Turczaninow's name to the Veracruz material, as is done in the above lectotypification, and specifically to exclude the Jameson collection, since it can be shown to differ from Turczaninow's description in several particulars.

Representative specimens: Veracruz, *Purpus 8313* (F, US), *16649, 16702* (US), *Rosas 1468* (A, MEXU). Chiapas, *Breedlove 8984* (F). Guatemala, *Standley 84567, 77239, 83171, 63031, 62909, 60341, 86575, 32525* (F), *63306, 64345* (F, MICH), Steyermark *34393* (F), *Williams et al. 25288* (F), *Molina et al. 15969* (F), *Aguilar 768, 216* (F), *von Turckheim 341* (MICH). Honduras, *Molina 7633, 7383* (F), *Standley and Molina 4521* (F). Costa Rica, *Brenes 12745* (F), *Standley and Valerio 43488* (F), *Tonduz 6792* (MO), *Standley 32852* (F).

5. Abutilon reventum S. Wats., Proc. Amer. Acad. Arts 21:418. 1886. Type: Chihuahua, Hacienda San José, 25 mi S of Batopilas, Aug 1885, *Palmer 56.* Holotype: GH!; isotype: US!.

Distribution: Known from southern Arizona, Sonora, and Chihuahua and in western Mexico as far south as Oaxaca, from elevations of 850–1800 m.

This species is distinctive in its sparsely viscid to glabrate and often darkly pigmented stems and its rounded fruits with more or less obtuse mericarps (fig. 4, B).

Representative specimens: Arizona, *Gould 3303* (TAES), *Pinkava and Lehto 6255* (ASU). Sonora, *White 2770, 4163, 3518* (MICH), *Phillips 467* (MICH). Chihuahua, *Palmer 56* (MICH). Durango, *Palmer 499* (F, MO, UC). Sinaloa, 31 Oct 1904, *Brandegee s.n.* (UC). Jalisco, *Fryxell 1035* (BH, CTES, DH, GH, pf), *Fryxell, Bates and Blanchard 1591, 1600* (BH, pf), *1599* (BH, TEX, pf). Guerrero, *Fryxell and Bates 2171* (BH, ENCB, pf). Oaxaca, *Fryxell 1150* (TEX, pf).

6. Abutilon sonorae A. Gray, Smithsonian Contr. Knowl. 5(6):23. 1853. Type: Sonora, Sonoita River, *Wright 899.* Holotype: GH! isotype: NY!

Distribution: Known from southern Arizona, western Texas, Sonora, and Chihuahua, and from an isolated collection in Guerrero, mostly at elevations of 350–1400 m.

This species is characterized by long, spreading hairs 2–3(–4) mm long on the stems and petioles (fig. 4, E), especially in the lower part of the plant (often lacking in the inflorescence), and by its frequently trilobed leaves (fig. 4, F).

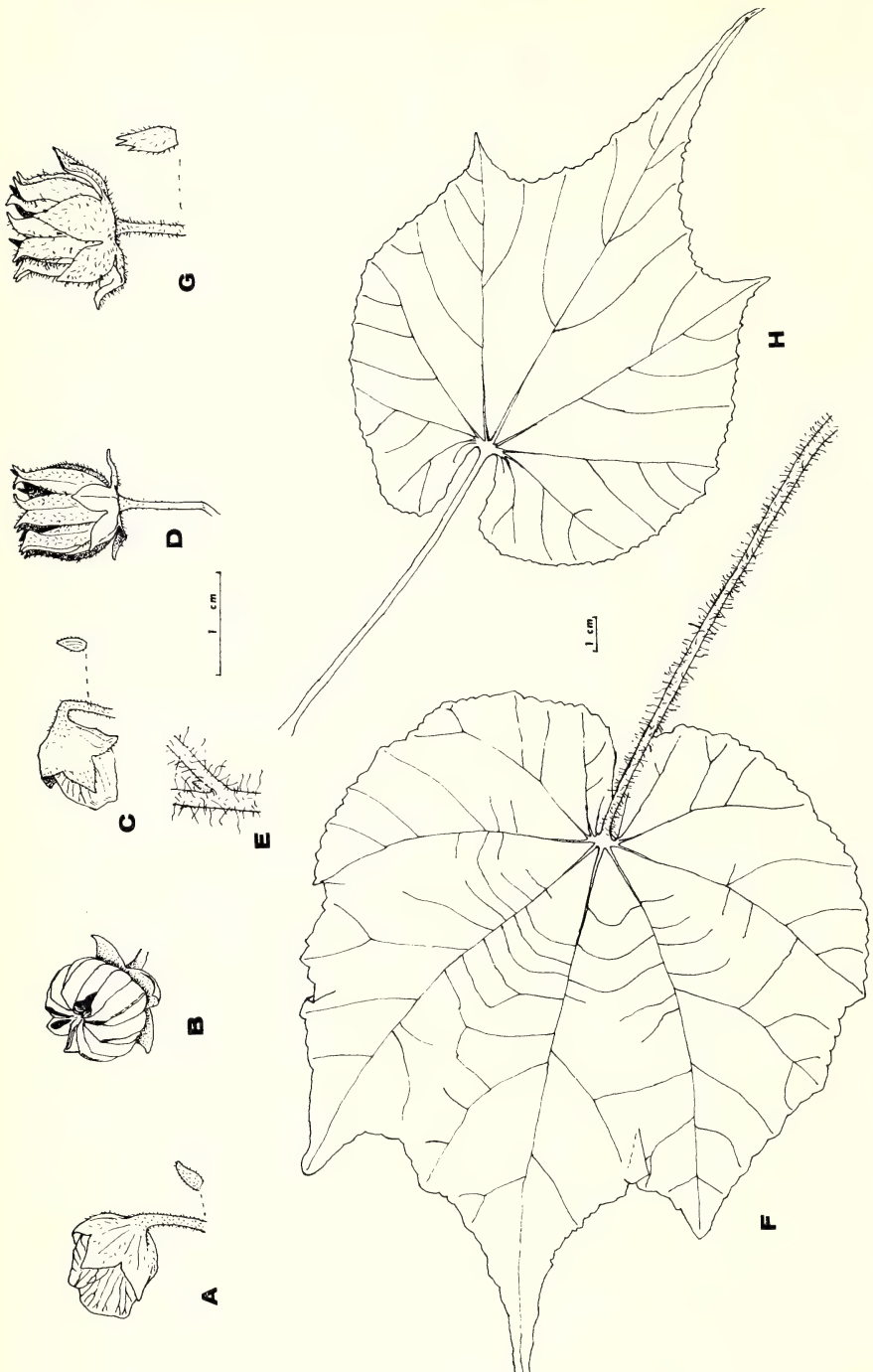


FIG. 4. A–B, *Abutilon reventum*. A, bud and floral bract (*Fryxell 1150*); B, fruit (*Fryxell and Bates 2171*); C–F, *Abutilon sonorae*. C, bud and floral bract (*Wiggins 7017*); D, fruit (*Shreve 6643*); E, stem and petiole, illustrating nature of vestiture (*Shreve 6643*); F, leaf (*Wiggins 7017*); G–H, *Abutilon xanti* (*Fryxell 1000*). G, fruit and floral bract; H, leaf.

REPRESENTATIVE SPECIMENS: Texas, *Correll 15090* (LL). Arizona, *Thornber 7582* (TAES), *Peebles 8993* (F). Sonora, *Drovet and Richards 3507, 3749* (F), *White 4681* (MICH), *Wiggins 7017, 7478* (MICH), *Muller 3615* (MICH), UC), *Shreve 6643* (MICH), *Wiggins and Rollins 373* (MICH, MO). Chihuahua, *Pringle 329* (F, MO) *944* (MO, MSC, UC), *Gentry 2891* (DES, F, MO, UC), *Palmer 171* (MICH). Guerrero, *Palmer 45* (F, LL, MO, UC).

7. ABUTILON XANTI A. Gray, Proc. Amer. Acad. Arts 22:301. 1887. TYPE: Baja California, Cape San Lucas, *L. J. Xantus 9*. Holotype: GH!; isotypes: NY! US!.

Abutilon carterae Kearney, Madroño 12:114. 1953. TYPE: Baja California (Distrito del Sur). Arroyo de Tabor, Sierra de la Giganta, W of Puerto Escondido, *Carter and Kellogg 2871*. Holotype: CAS!; isotypes: UC!, US!.

DISTRIBUTION: Baja California from the vicinity of Loreto south to the end of the peninsula, at elevations up to 650 m.

In describing *Abutilon xanti,* Gray noted its alliance to *A. sonorae* and *A. reventum,* and Baker (1893, p. 73) commented on the same similarity. Standley (1923) also reflected this alliance by the placement of *A. xanti* in his key to the Mexican species of *Abutilon* (loc. cit., p. 749). Kearney's description of *A. carterae* noted a resemblance of his species to *A. sonorae* but made no reference to Gray's species. In his key to North American species of *Abutilon,* Kearney (1955) recognized both *A. xanti* and *A. carterae* and distinguished them in his key at couplet 38, whether the calyx is more or less than ⅔ the length of the mature fruit. Wiggins (1964) used the same distinction, modified to: calyx "much shorter than" vs. "nearly equaling or surpassing" the mature carpels. The original description of *A. carterae* states that the calyx is 0.6 times the length of the fruit and that of *A. xanti* says the calyx is nearly equal to the fruit. An examination of the holotype of *A. xanti* reveals that the calyx varies in length from half that of the fruit to nearly equaling the fruit. Kearney's criterion is thus found to be artificial in this instance (although otherwise useful in distinguishing species), and an examination of a range of material indicates that the plants that occur in Baja California may be encompassed in a single species, the earlier name for which is *A. xanti.*

This species is somewhat variable and is similar to *A. sonorae,* both having often trilobed leaves (fig. 4, H) and relatively pale flowers. The densely soft-tomentose stems and petioles of *A. xanti* contrast with the long-hirsute stems and petioles of *A. sonorae.* These species differ in other characters as well, the calyx and petals in *A. xanti* being longer (fig. 4, G), the staminal column shorter, and the floral bracts more commonly dentate than in *A. sonorae.*

REPRESENTATIVE SPECIMENS: Baja California, *Carter and Sharsmith 4258* (UC), *Carter and Sousa 5177* (UC, pf), *Carter and Ferris 4087, 4077* (UC, pf), *Carter, Alexander, and Kellogg 2055* (LL, UC, US),

Gentry 4111 (DES), *Moran 7331* (MICH, UC), *Fryxell 1982* (CTES, ENCB, pf), *1990* (BH, CTES, ENCB, pf).

8. **Abutilon macvaughii** Fryx., sp. nov. sectionis *Armatae* (fig. 5, F–G). Frutex usque ad 3 m altus. Caules minute stellato-pubescentes pilis dispersis, ca 0.1 mm diam. Folia profunde cordata, ovata, acuminata, subintegra, 9–11-pedatinervata, usque ad 14 cm longa, 10 cm lata, discoloria, supra viridia et glabrata, infra minute molli-pubescentia et albida. Petioli usque ad 10 cm longi, pubescentiis caulis similis. Stipulae auriculato-amplexicaules, late falcatae, 18–20 mm longae, 8–10 mm latae; stipulae inflorescentiae aliquantum breviores sed 3–4-laciniatae et velut pseudo-involucellum binatim alabastra includentes. Inflorescentia racemosa vel paniculata. Pedicelli 2–20 mm longi, minute puberuli. Calyces ca 10 mm longi, minute puberuli, plus minusve semi-divisi; lobi ad basim 5–6 mm lati, aliquantum longiori quam latiori, sine nervis prominentibus, demum ad basim gibbosescens. Petala flavida, 18–20 mm longa, 10–15 mm lata, unguibus 2.5–3.0 mm latis, intus glabra praeter dense pubescentia in marginibus unguium, extus stellato-pubescentia ad basim, ceterum glabra. Columna staminalis pallida, 6 mm longa, 4 mm diam. ad basim, sursum decrescens ad 1 mm diam., stellato-pubescens praeter ad apicem. Filamenta pallida, 3–4 mm longa, erecta, ex apice columnae omnino exorientia; antherae $<$ 1 mm longae, pallidae; pollen luteum, globosum, spinosum. Styli 10, androecium excedentes, glabri, viridi-pallidi; stigmata capitata, purpurata. Fructus dense et minute stellato-pubescentes; mericarpia 10, 8–9 mm longa (sed immatura), ad apicem acuta.

Type: Mexico, Jalisco, 8 km E of Chamela, elev. 30–50 m, shrub—2–3 m high, abundant, flowers bright yellow, 8–10 Dec 1970, *R. McVaugh 25118*. Holotype: MICH; isotypes: pf, and to be distributed by MICH. Paratypes: Jalisco, Estación Biologica de Chamela de la UNAM, alt. 80 m, vegetación secundaria, arbusto de 1.5–2.5 m de alto, 7 Mar 1973, *Souza* (con *Perez y Sarukhán*) *3889* (MEXU); Chamela, alt. 90 m, flores amarillas, 9 Mar 1973, *Souza* (con *Perez y Sarukhán*) *3913* (MEXU). Guerrero, Tecpan, alt. 150 m, petit arbuste, fleurs jaunes, sol granitique, 12 Dec 1899, *E. Langlassé 742* (US).

Distribution: Known only from the specimens cited above from coastal Jalisco and Guerrero, at low elevation. The specimen of Langlassé from Guerrero probably belongs in this species. The specimen is incomplete, however, so this conclusion is only tentative. It differs in certain characters from the Jalisco material; if these differences prove to be real and consistent on the basis of additional material from coastal Guerrero, they do not appear to merit recognition at more than subspecific rank.

This species is distinctive for its large yellow flowers and its well developed floral bracts (fig. 5, F). The flowers are reported (M. Sousa, in litt.) to be visited by female carpenter bees (*Xylocopa mexicanorum* Cockerell).

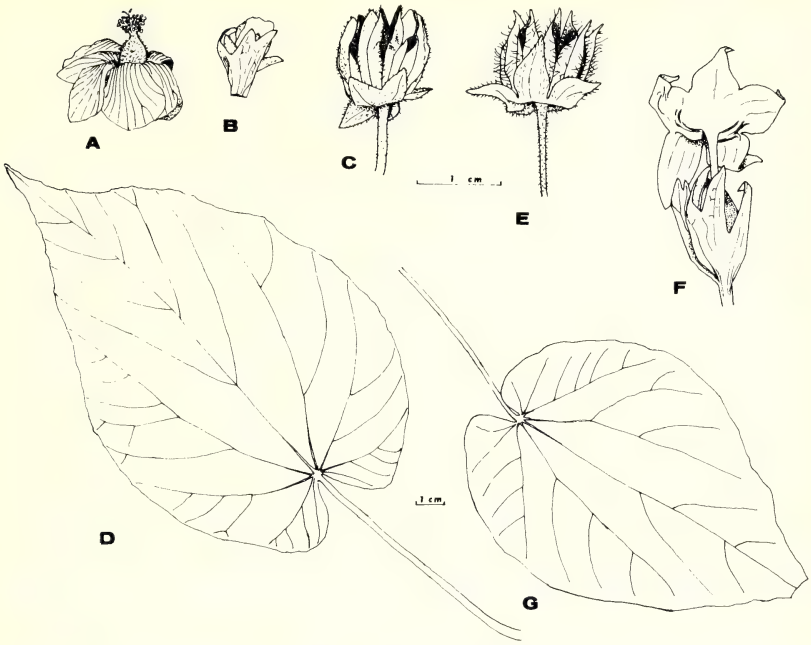


FIG. 5. A–D, *Abutilon andrieuxii* (*Ton 3772*); A, flower; B, bud enclosed within floral bract; C, fruit; D, leaf; E, *Abutilon haenkeanum,* fruit (*Fryxell 1716*). F–G, *Abutilon macvaughii* (*McVaugh 25118*). F, calyx and floral bracts; G, leaf.

9. ABUTILON ANDRIEUXII Hemsl., Diagn. Pl. Nov. 24. 1879. TYPE: Oaxaca: Tlacolula, *Andrieux 522*. Holotype: G, photo F!.

Abutilon reticulatum Rose, Contr. U. S. Natl. Herb. 5:171. 1899. SYNTYPES: Oaxaca, Monte Alban, *Pringle 6062* (F! MICH! MO! MSC! UC! US!); in cult., *Rose 1122* (MO! NY! US!).

Abutilon calderonii Standl., J. Wash. Acad. Sci. 14:99. 1924. TYPE: El Salvador, San Salvador, *Calderón 1639*. Holotype: US!

DISTRIBUTION: Oaxaca and Chiapas, southward to Guatemala and El Salvador, at elevations of 300–1800 m.

This species and *A. haenkeanum* are distinguished by their orange, reflexed petals with minute external pubescence and by their very short filaments, 1.0–1.5 mm long (fig. 5, A). The characters distinguishing *A. andrieuxii* and *A. haenkeanum* are given in the key (cf. figs. 5, C and 5, E).

REPRESENTATIVE SPECIMENS: "Nova Hispania", *Sessé, Mociño, Castillo and Maldonado 3475* (F). Oaxaca, *Fryxell and Bates 904* (BH, pf). Chiapas, *Ton 3772* (F, pf), *3909* (CAS, pf), *Fryxell and Bates* 894 (ARIZ, BH, CTES, L, MEXU, pf), *901* (BH, CAS, CTES, pf). Guatemala, *Williams, Molina and Williams 22443* (F), *Standley 61353* (F), *Kellerman 7804* (F), anonymous *1713* (F). El Salvador, *Williams and Molina 15238* (F), *Tucker 930* (LL).

10. Abutilon haenkeanum Presl, Rel. Haenk. 2:115. 1835. Type: In terris mexicanus occidentalibus, *Haenke s.n.* Holotype: PR!; isotypes: MO!, W, as photo F!.

Sida presliana D. Dietr., Syn. Pl. 4:856. 1847 [based on *A. haenkeanum*].

Distribution: In western Mexico from Sinaloa to Guerrero, at elevations up to 450 m.

This species and *A. andrieuxii* are distinctive for their orange, reflexed petals with minute external pubescence and for their very short filaments, 1.0–1.5 mm long. The characters distinguishing *A. haenkeanum* and *A. andrieuxii* are given in the key (cf. figs. 5, C and 5, E).

Representative specimens: Sinaloa, *Gentry 5644* (DES, MICH, NA). Colima, *Fryxell 1049* (BH, MEXU, MICH, US, pf), *1054* (CTES, MICH, NY, pf). Michoacán, *McVaugh 22604* (ENCB), *Fryxell 1716* (ASU, SMU, SD, pf), *Hinton 16214* (TEX). Guerrero, *Paray 1829* (ENCB), *Hinton 11783* (TEX).

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A NEW SPECIES OF TRIFOLIUM (LEGUMINOSAE) FROM BAJA CALIFORNIA, MEXICO

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Currently, my interest in *Trifolium* centers about sect. *Involucrarium* Hooker. Among material from Baja California, the following taxon, which is evidently new, has come to light. The plant was first collected by I. L. Wiggins and D. Demaree in 1930 but has been collected several times since. I take great pleasure in naming this clover after Dr. Wiggins because of his great interest in the region.

The peninsula of Baja California is well known for its high incidence of endemism (Shreve and Wiggins, 1964), so it is not altogether surprising that a new clover should be found. The stipules of *T. wigginsii* resemble those of *T. variegatum* Nutt. or related species, but the habit and involucral characters resemble those of *T. pinetorum* Greene of Arizona and New Mexico.

Trifolium wigginsii J. M. Gillett, sp. nov. *Trifolium* perenne radicibus palaribus, caulibus prostratis ramosis, stipulis ovatis persistentibus, foliolis obovatis vel cuneatis, capitulis semiglobosis, pedunculis longioribus quam foliis, involucrarium divisio in segmentis oblongis, triaristatis, lobis calycis brevioribus quam tubis.

Type: Mexico, Baja California, Sierra San Pedro Martir. Abundant, forming sod in dry meadow west of Vallecitos, 30°00′N, 115°28′W, 2450 m, 23 Aug 1968, *Reid Moran 15400*. Holotype: RSA!; isotype: SD!

Glabrous tap-rooted perennial, tap-root bearing numerous fine roots and a multicipital crown of spreading prostrate stems, 0.5–6.0 dm long, these often branched and when buried often behaving like rhizomes and rooting at the nodes, internodes of well-developed stems 1.5–3.0 cm long. Leaves with three leaflets, petioles 1.2 (0.3–2.0) cm long, overtopped by the heads, petiolules 0.25–0.5 mm long, blades 0.46 (0.2–0.7) cm long, 0.3 (0.15-0.4) cm wide, slender cuneate to obovate, truncate to rounded, or slightly retuse, minutely apiculate, the margins dentate to serrate, the abaxial face with prominent light-colored veins, often bifurcating towards the tips and terminating in the teeth. Stipules 0.4–0.7 cm long, ovate with attenuate tips and somewhat lacerate margins, the pairs united ⅓ of their length and surrounding the stem, pale green below, darker green above, veiny, later chartaceous and persistent. Inflorescence capituliform, hemispherical, occasionally abruptly turned upwards at the tip of the peduncle, of 10–15 flowers, peduncles 3.6 (1.0–6.0) cm long. Involucre 0.4–0.5 cm high, with 7–9 oblong lobes, cleft to within ¼ their length to the base, apex usually with 3 acute to acuminate teeth but sometimes these a trifle irregular and occasionally with 1–2 lateral teeth, veins anastomosing and terminating in the teeth. Flowers in 1–3 whorls, secondary whorls subtended by a mini-involucre of blunt, hyaline, fused bracts, each flower borne on an extremely short pedicel (essentially sessile), the standard, wings, and keel white or lavender towards the tips, or the wings reddish-violet and the keel purplish-violet. Calyx glabrous ca 1 cm long, slightly oblique, the tube 3 mm long, pale green to white with 5 main veins extended into the lobes and 5 smaller sinal veins uniting with the lateral lobal veins below the rounded to acute sinus, lobes ca 2 mm long, almost equal, subulate and probably green. Standard tubular, elliptic when flattened, 1.2 cm long, 0.4 cm wide, with numerous parallel veins, dichotomising apically, the upper third flared upwards. Wings slightly shorter than the banner, blades 0.5–0.6 cm long, equal to the claw, this lightly united to that of the keel, the vesicular processes inflated; keel 1.5 mm shorter than the wings, the blade

FIG. 1. *Trifolium wigginsii* J. M. Gillett. a, habit; b, late season prostrate stem; c, head; d, involucre; e, calyx; f, standard (flattened); g, wing petal; h, keel petal; i, ovary; j, staminal tube. (a from *Moran 15400*, SD, RSA; b from *Wiggins and Demaree 4986*, DS; c–j from *Moran and Thorne 14171*, RSA.)

oblong, oblique, 3.0–3.5 mm long, often purple-violet. Stamens fused into the staminal tube most of their length, the anthers 0.5 mm long, that of the free stamen similar. Ovary at anthesis ca 3 mm long, glabrous; ovules 2. Somewhat immature fruit oblong, 2 mm long, 1.5 mm wide, containing two slightly flattened seeds.

PARATYPES: All from Mexico, Baja California, Sierra San Pedro Martir. Granitic slope with grassy openings, rocky knolls in a forest of *Pinus jeffreyi, P. murrayana, Populus tremuloides, Quercus,* and *Ceanothus,* near the settlement of Vallecitos in the vicinity of Ensenada, 8000 ft, 21 Sep 1968, *D. E. Breedlove 16359* (CAS); Vallecitos meadow, 1 mi S of road to Observatory, ca 8200 ft, in full sun, open meadow with *Leptodactylon melingii, Ivesia aryrocoma, Astragalus circumdatus,* and other perennial forbs, several grasses, stems strictly prostrate, the plants forming dense small mats, petals white with faint lavender tinge near the tips of some, 18 Jun 1971, *I. L. Wiggins 21458* (DS); in sandy wash, Vallecito, calyx reddish, banner white, wings red-violet, keel red-purple, near 31°00′N, 115°28′W, ca 2475 m, 9 Aug 1969, *H. V. Witham 369* (RSA,SD); occasional in arroyo, Jeffrey pine forest, Yerba Buena, near 31°00′N, 115°27′W, ca 2500 m, 16 Aug 1967, *R. Moran and R. F. Thorne 14171* (RSA,SD); common in meadow, La Encantada, near 30°55′N, 115°24′W, ca 2200 m, 18 Aug 1967, *R. Moran and R. F. Thorne 14303* (RSA,SD); fairly common, forming mat in wet sand of arroyo, Jeffrey pine forest, Yerba Buena, near 31°00′N, 115°27′W, ca 2500 m, 16 Aug 1967, *R. Moran and R. F. Thorne 14167* (RSA); mid-vegetative stages, small-leaved, to 6 in stems; upper San Jose Creek bottom (water 10–20 ft below sandy bed), 0–3 mi beyond end of road into N end of High Sierra San Pedro Martir, 7200–7700 ft, steep to slightly sloping granite walls, aspen, incense cedar, white fir, *Aquilegia,* etc., and *Holodiscus* but no chaparral, Jeffrey pine forest border, 6 Jul 1962, *J. D. Olmsted 4567* (RSA); dry hillside, upper end of flats, La Encantada, 7250 ft, 22 Sep 1930, *I. L. Wiggins and D. Demaree 4986* (DAO, DS, RSA, US).

I have refrained from selecting *Wiggins and Demaree 4986* as the type even though I am naming the species after Wiggins and in spite of the several replicates, because this collection consists of stem bearing flowers and does not satisfactorily show the distinctive tap root and habit of the plant.

Trifolium worskjoldii Lehm. also is found in La Encantada region (*Wiggins and Demaree 4908, Moran 22154*) but is apparently restricted to streams running through a meadow; *T. wigginsii,* however, is a species of dry habitats, occupying dry gravel and hillsides. I should judge that it occupied a very similar habitat to *T. pinetorum* Greene.

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SYSTEMATICS OF THE ERICAMERIA CUNEATA COMPLEX (COMPOSITAE, ASTEREAE)

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Ericameria cuneata (Gray) McClatchie is a highly variable, wide ranging taxon occurring from the northern Sierra Nevada and Coast Ranges south of Monterey, California, to central Baja California and southeastern Arizona. Populations of *E. cuneata* are usually restricted to rocky outcrops at elevations from 750 to 2750 m and occupy diverse vegetation zones ranging from creosote bush scrub in the Mojave Desert to yellow pine forests in the northern Sierra.

Ericameria cuneata was described by Gray (1873) as *Haplopappus cuneatus* and based on radiate specimens collected in the Sierra. In 1876 Gray described *Bigelowia spathulata* and noted its resemblance to *H. cuneatus* but distinguished it from the latter on the basis of eradiate heads. nonglutinous and obscurely punctate foliage, noncarinate phyllaries, shorter more silky achenes, and clavate pappus bristles. In 1886, admitting some eradiate taxa to *Haplopappus,* Gray placed *B. spathulata* and *B. rupestris* Greene (1881; Arizona) in synonymy with *H. cuneatus.* Greene (1895) treated *Ericameria* as congeneric with *Chrysoma.* Eastwood (1905), accepting Greene's treatment, described *C. merriamii* from material collected in Kern County, California. Hall (1928), the last monographer of the group, having only limited material available, viewed *B. spathulata, B. rupestris,* and *C. merriamii* as taxonomically insignificant variants of *H. cuneatus.*

Materials and Methods

Field observations and collections were made during the early fall months of 1972 and 1973. Usually, five to ten plants were collected from each population. Morphological analyses also utilized specimens borrowed from the following herbaria: ARIZ, ASU, CAS, COLO, DAV, DS, F, GH, JEPS, LL, MICH, MO, NY, OSC, PH, POM, RSA, SD, SMU, TEX, UC, UCSB, US, UTC, WS, WTU. Leaf measurements and shapes were based on the largest leaf per specimen; length measurements included the petiole, and width was measured at its widest point. Number of disk florets per head represents an average based on counts from three heads for each plant. Means, ranges, and standard deviations for each population are based on measurements from 10 to 20 individuals.

Chromosome number determinations (all $n = 9$) were made for the collections cited below using aceto-carmine squashes of pollen mother cells from bud material that was collected in the field and preserved in modified Carnoy's solution (chloroform:ethanol:acetic acid, 4:3:1 v/v). Voucher specimens are in LL; collection numbers are mine. *Ericameria cuneata* var. *cuneata*: CA, Kern Co., 11 mi. NW of Tehachapi, *1533*; Tuolumne Co., along the road to Hetch-Hetchy Reservoir, 9.7 mi. from

Jct. of 120 X Rd. to Hetch-Hetchy, *1521*; *E. c.* var. *macrocephala*: CA, San Diego Co., Desert View, Mt. Laguna, *1538*; *E. c.* var. *spathulata*: AR, Santa Cruz Co., Sycamore Canyon, *1541*.

Results and Discussion

Ericameria cuneata in the northern Sierra Nevada occurs at ca 2150 m in association with *Pinus ponderosa, P. jeffreyi, Libocedrus decurrans, Quercus kelloggii,* and *Arctostaphylos* spp., grows as a rounded shrub less than 4 dm tall, and has small, sessile, cuneate leaves (fig. 1, A). Populations in the central and southern Sierra and the San Bernardino and San Gabriel Mountains range down to 1050 m, usually occur with foothill woodland taxa, and have somewhat larger, cuneate leaves. The

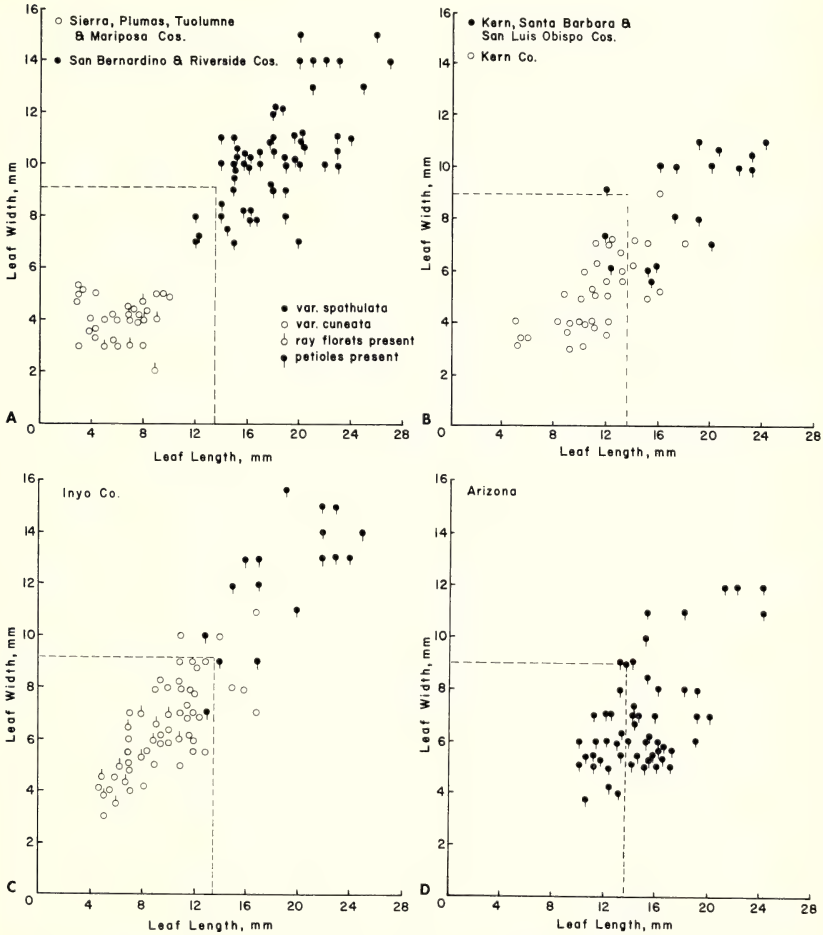

Fig. 1. Scatter diagrams showing variation in leaf size, presence of petioles, and presence of ray florets in populations of *Ericameria cuneata*. The dash lines are included as reference points.

cuneatas on the eastern face of the Sierra and in the White and Inyo Mountains, where the habitat is more xeric and supports *Pinus monophylla, Juniperus* sp., *Chrysothamnus teretifolia,* and *Artemisia* sp., often form semiprostrate, mat-like shrubs to 1 m in diameter and have sessile, cuneate but broader leaves than those in the central Sierra (fig. 1, C).

In southeastern California *Ericameria cuneata* is associated with Joshua tree woodland and creosote bush scrub, grows upright to 1 m tall, and has large, petiolate, spatulate leaves (12–30 mm long; fig. 1, A). Similarly, the Arizona populations occupy xeric sites but have somewhat smaller, more slender petiolate, spatulate leaves (fig. 1, D). The cuneatas in Baja California are primarily associated with pinyon-juniper woodland and have spatulate leaves that exhibit the same size range as the Arizona populations but have shorter, stouter petioles. The Arizona and Baja California cuneatas are smaller in habit than those in the Mohave desert.

On the basis of habitat, leaf shape, and to some extent leaf size, two taxa can be delimited among the aforementioned populations. One occurs at higher elevations, is adapted to cooler, more mesic habitats, and has smaller, cuneate, sessile leaves; the other has larger, spatulate, petiolate leaves and is adapted to xeric areas.

These taxa are fairly distinct throughout most of their ranges, but they intergrade in areas of sympatry, notably in the Tehachapi and Greenhorn Mountains in Kern County, California (fig. 1, B); this corresponds to a region where their usually distinct habitats gradually intergrade (Stebbins and Major, 1965). Populations that occur in the Coast Ranges are morphologically similar to those in the transition zone (fig. 1, B).

On the basis of their morphological variation pattern, these entities are treated as varieties. The correct name for the cuneate-leaved, more mesic taxon is *E. cuneata* var. *cuneata*; that for the more xeric element is *E. cuneata* var. *spathulata*. These taxa are treated formally in the systematic section of this paper. A summary of variation in leaf size and shape for the two varieties is given in Figure 2.

Ray florets are lacking in var. *spathulata,* while they are sporadically present in many populations of var. *cuneata* and regularly occur in the northernmost populations of this variety. Although this character is of little taxonomic value, it may be of considerable adaptive value in reproductive biology, especially in the northern populations. Both varieties have similar numbers of disk florets per head except for the northern populations of var. *cuneata* and the Arizona populations of var. *spathulata* that have fewer (fig. 3).

Populations of *E. cuneata* in the Laguna Mountains differ drastically from the aforementioned varieties in having fewer but much larger heads with considerably more florets (fig. 3) and more numerous phyllaries. Since these populations are well isolated geographically and are distinct morphologically, I propose that they be recognized as a third variety of

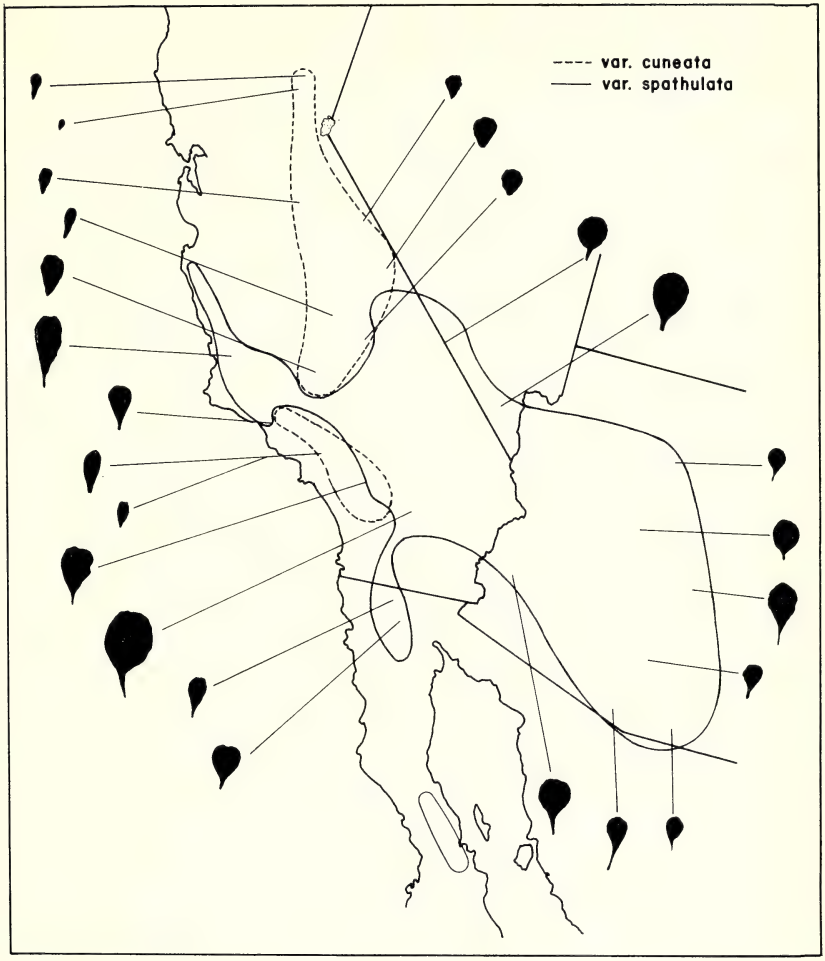

FIG. 2. Leaf silhouettes depicting variation in leaf size and shape throughout the ranges of *Ericameria cuneata* var. *cuneata* and var. *spathulata*.

E. cuneata, namely var. *macrocephala.* Occurrence of occasional teratological heads in *macrocephala* that have the appearance of being aggregations of "partly-fused" smaller heads suggests that this variety evolved from an ancestral form having many, small, cymosely arranged heads much like present day var. *cuneata.*

Karyological studies show that the chromosome number for all varieties is uniformly $n = 9$, which agrees with an earlier report (Solbrig et al., 1964).

TAXONOMIC TREATMENT

ERICAMERIA CUNEATA (Gray) McClatchie, Erythea 2:124. 1894.

Evergreen shrubs 1–10 dm tall, intricately branched, usually rounded;

stems to 3 cm thick at base, weakly ascending to erect, young stems green or tan becoming gray on older branches; leaves cuneate to spatulate, 2–25 mm long, 2–16 mm wide, petiolate or sessile, apices mucronate or retuse, resinous dots and usually a heavy resinous coat on both leaf surfaces; capitulescence of rounded, compact, cymose clusters, up to 8 cm broad and 5 cm high; involucres turbinate to subcampanulate, 4–14 mm broad, 6–12 mm high, phyllaries imbricate, in 3–6 graduated series, lanceolate to obovate, chartaceous, glabrous, the apices acute to obtuse or sometimes acuminate, the margins membranous, outer phyllaries 1–2 mm long, 0.5–1.5 mm wide, often resinous, inner phyllaries 2.5–6.0 mm long, 1.7–2.0 mm wide; capitula usually eradiate, but radiate in some populations, ray florets 0–7; ray corollas ca 7 mm long, glabrous, occasionally with sparse resinous dots, ligules ovate, ca 4 mm long, 1.5 mm wide; disk florets 7–70, disk corollas ca 5.5 mm long, glabrous, the tube gradually ampliate into a cylindrical limb, lobes triangular acute, ascending or somewhat spreading, ca 0.7 mm long; pappus identical on disk and ray florets, composed of ca 30 subequal, setose, capillary bristles per floret, brownish-white, nearly as long as the disk corollas; achenes prismatic, 2.5–3.0 mm long, usually 5-ribbed, pubescent, often densely so with silky ascending twin hairs to 0.8 mm long; $n = 9$.

Key to varieties of *Ericameria cuneata*

a. Disk florets 33 or fewer per head; widely distributed in California, Arizona, Baja California. . . . . b.

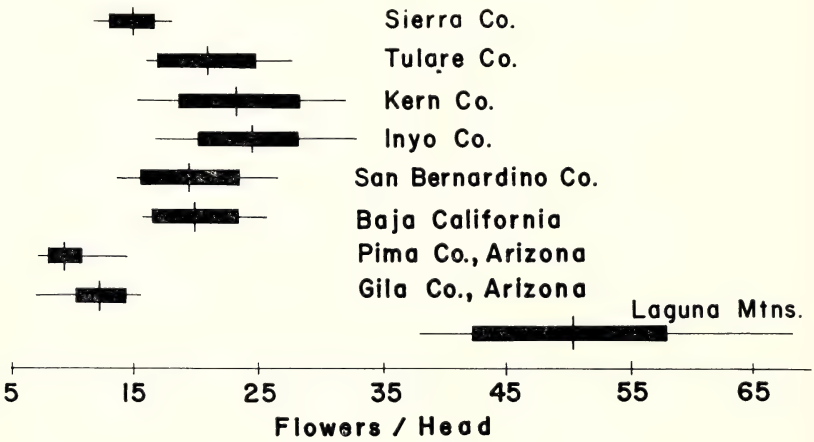

Fig. 3. Variation in disk floret number of representative populations of *Ericameria cuneata*. The top four populations represent var. *cuneata*, the next four represent var. *spathulata*, while the lowermost represents individuals from the Laguna Mtns. The mean number of florets per head for a sample is given by the vertical line, the range by the horizontal line, and two standard deviations by the bar. The standard errors of the means from top to bottom, respectively, are: 0.36, 0.43, 0.36, 0.30, 0.42, 0.25, 0.11, 0.58, 0.83.

b. Leaves cuneate, sessile, largest ones 3–14(18) mm long, 2–9(12) mm wide. . . . . 1. var. *cuneata*

bb. Leaves spatulate, usually with a distinct petiole, the largest ones (9) 12–25 mm long, 4–16 mm wide. . . . . 2. var. *spathulata*

aa. Disk florets 36 or more per head; restricted to the Laguna Mountains, San Diego County, California. . . . 3. var. *macrocephala*

1. Ericameria cuneata (Gray) McClatchie var. cuneata.—*Haplopappus cuneatus* Gray, Proc. Amer. Acad. Arts 8:635. 1873.—*Aster cuneatus* (Gray) Kuntze, Rev. Gen. Pl. 1:317. 1891.—*Chrysoma cuneata* (Gray) Greene, Erythea 3:11. 1895. Type: In his protologue, Gray cited, "California, in 'Bear Valley, alt. 4,500 feet, Sept.,' Kellogg, Bolander, etc.; no. 402 of Kellogg and Harford's distribution." Two of the collections cited by Gray are in GH: *Bolander* with locality as cited in protologue and *Kellogg and Harford 402* without locality data. The latter is annotated "n. sp." in Gray's hand (fide Rollins, pers. comm.). I here designate *Kellogg and Harford 402* (GH!) as lectotype because Gray obviously saw this specimen and several herbaria have duplicates of it (CAS!, PH!, NY!, US!).

Chrysoma merriamii Eastw., Bull. Torrey Bot. Club 32:215. 1905. Type: California, Kern Co., Caliente Creek, 12 Oct 1902, *Merriam s.n.*, Holotype: CAS!

Distribution (fig. 4): Plumas Co. south through Sierra Nevada and into the Topatopa Mts., Ventura Co., San Gabriel Mts., Los Angeles Co., White and Inyo Mts., Inyo County. Locally common, usually restricted to granitic outcrops at 1050–2725 m. Mid-August to December.

This taxon is quite variable in habit, leaf size, and occurrence of rays. Generally, plants in more xeric areas have larger leaves. Ray florets are usually present in the northernmost populations and sporadically occur elsewhere. This variety intergrades with *E. c.* var. *spathulata* where their ranges overlap.

2. Ericameria cuneata (Gray) McClatchie var. spathulata (Gray) Hall, Univ. Calif. Publ. Bot. 3:52. 1907.—*Bigelowia spathulata* Gray, Greene var. *spathulata* (Gray) Greene, Erythea 3:11. 1895.—*Haplopappus cuneatus* (Gray) McClatchie var. *spathulatus* (Gray) Blake, Contr. U. S. Natl. Herb. 23:1849. 1926. Type: Baja California, Tantillas Canyon (also spelled Cantillas and located in Sierra Juarez Mts., ca 128 km SE of San Diego, near 32°15′N, 116°W fide Ewan, 1937), Sep 1875, *Palmer 133*. Holotype: GH!; isotypes: MO! NY!

Bigelowia rupestris Greene, Bot. Gaz. (Crawfordsville) 6:183. 1881. Type: Arizona, Coconino Co., rocky summits of San Francisco Mts., 1 Nov 1880, *Greene s. n.* Lectotype (here designated): GH! isotypes: F! K, POM! [A search at NDG yielded no type material (Crovello, pers. comm.).]

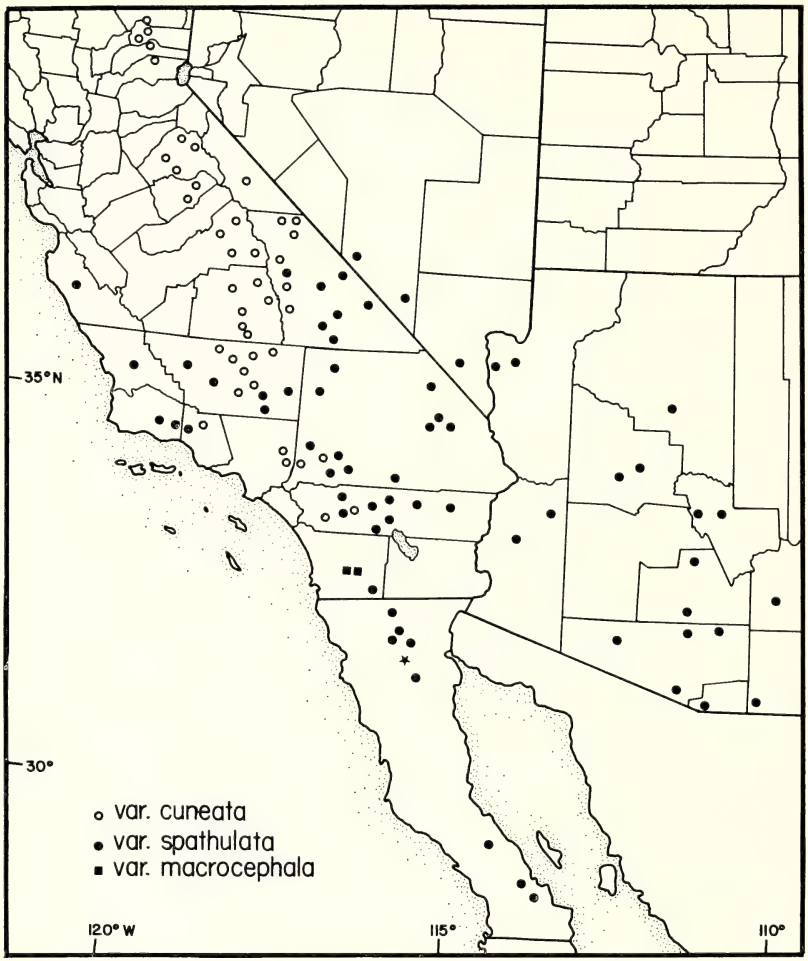

Fig. 4. Distribution of the three varieties of *Ericameria cuneata*. The star indicates the type locality of var. *spathulata*.

Distribution (fig. 4): Coast Ranges, Monterey Co., California, south to Sierra San Borja in Baja California and east to Nye Co., Nevada, and Graham Co., Arizona. Locally common, usually on rock outcrops, 750–1850 m. August to December.

This variety is eradiate and variable in leaf size and habit. It occurs predominantly in xeric habitats.

3. **Ericameria cuneata** (Gray) McClatchie var. **macrocephala** Urbatsch, var. nov. Capitula 6–10 mm lata 9–12 mm alta 36–70 flora; flores radiati nulli; involucrum 4–6-seriatum; phyllaria inaequalia.

TYPE: California, San Diego Co., Desert View, Mt. Laguna, ca 1.2 mi N of the town of Mt. Laguna, crevices of steep east-facing outcrop, shrubs to 4 dm tall, eradiate, ca 1850 m, 2 Oct 1974, *Urbatsch and Clark 1538A*. Holotype: LL!; isotypes: LSU!, UC!

DISTRIBUTION (fig. 4): endemic to the Laguna Mountains in San Diego Co. This variety grows among boulders, from crevices in granitic outcrops, or, occasionally, rooted in rocky soil in chaparral near the yellow pine vegetational zone. Mid-September to December.

LIST OF EXSICCATA

Lists of nearly 500 herbarium specimens that formed the basis for much of this study are available from the author.

ACKNOWLEDGMENTS

I thank Dr. J. Bacon and Mr. R. Hartman for reading and criticizing the manuscript and Prof. M. C. Johnston for providing the Latin diagnosis. I am also grateful to Profs. R. Ornduff and R. Rollins for searching Gray's and Bolander's original correspondence for information concerning the type locality of *Ericameria cuneata,* to Prof. T. J. Crovello for searching NDG for Greene's types and to herbarium curators for loans. Mr. J. Wussow was instrumental in gathering much of the data for this study, which was supported by NSF grant GB-40362 and a grant-in-aid of research from the Society of the Sigma Xi.

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SAXIFRAGA TEMPESTIVA (SAXIFRAGACEAE), A NEW SPECIES FROM THE PACIFIC NORTHWEST

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Taxonomic differences in *Saxifraga* have been based largely on plant habit, ovary position, and shape of the filaments, petals, and leaves. Little attention has been given to the nectary disc, although in a comparative study, this character proved to be especially useful in delineating a new species. *Saxifraga tempestiva* (fig. 1) is described as a new taxon from western Montana and is classified in sect. *Boraphila* subsect. *Integrifoliae*. To ascertain the relationships of the new species with its apparent allies in sect. *Boraphila*, a study was made using species in subsect. *Integrifolia* and in the closely related subsect. *Nivali-virginienses*.

Saxifraga tempestiva Elvander & Denton, sp. nov. Perennis, caudice erecto, bulbillis frequenter praedito; scapi 1.5–8.0(–10) cm alti, glabri vel pilis glanduliferis septatis usque ad 1 mm longis et cellulis purpureis terminantibus; folia anguste ad late obovata, 0.5–2.0(–3) cm longa, 0.2–1.5 cm lata, glabra, marginis integris ad minutis dentatis; inflorescentia floribus (1–)3–5(–10) composita, cymosa; bracteae integrae, lineares, 5–8 mm longae; pedicelli 0.5–1.0 mm longi; sepala ovata, 1–2 mm longa, viridia ad atropurpurea, horizontaliter patentia, basi parve connata; petala late elliptica a spatulata, 0.5–1.0 mm longa, alba, unguiculata, breviora quam sepalis; stamina sub anthesi sepalis subaequantia, filamentis 1–2 mm longis, albis; discum nectariorum ovario circumdatum, maculosum, purpureum ad atropurpureum sub anthesi, crassum, succulentum, fere sub fructificatione conspectum; carpella 2(raro 3–4), viridia ad integerrime rubelli-purpurea sub anthesi, basi libera, adaxialia, sed ad discum abaxialem nectariorum conjuncta; ovarium amplium, ¾ inferum sub anthesi, aspectu ½–¾ infero sub fructificatione; styli minuti, sub anthesi erecti, sub fructificatione recurvi; stigmata inconspicua; folliculi rubelli-purpurei, 2–3 mm longi, ex ovario marginibus adaxialibus ad basim stigmatum dehiscentes; semina sphaerica vel ovoidea longitudinaliter rugosa, brunnea, circiter 0.6 mm longa; $n = 5$.

Type: U.S.A., Montana, Deerlodge County, Anaconda Range, 15 mi southwest of Anaconda, ca 0.6 mi west of Storm Lake Pass at Goat Flat (Storm Lake Quadrat, T.4N., R.13W.), 2830 m, flowering and fruiting, 21 Jul 1974, *Elvander 492*. Holotype: WTU.

The specific epithet is derived from the Latin word "tempestivus" meaning early, opportune, or fit; the name seems appropriately applied to one of the first alpine species to appear when the snow recedes and to one which seems well suited to the habitats in which it is found.

Distribution (fig. 2): Bitterroot Mts. and the Anaconda Range in Montana.

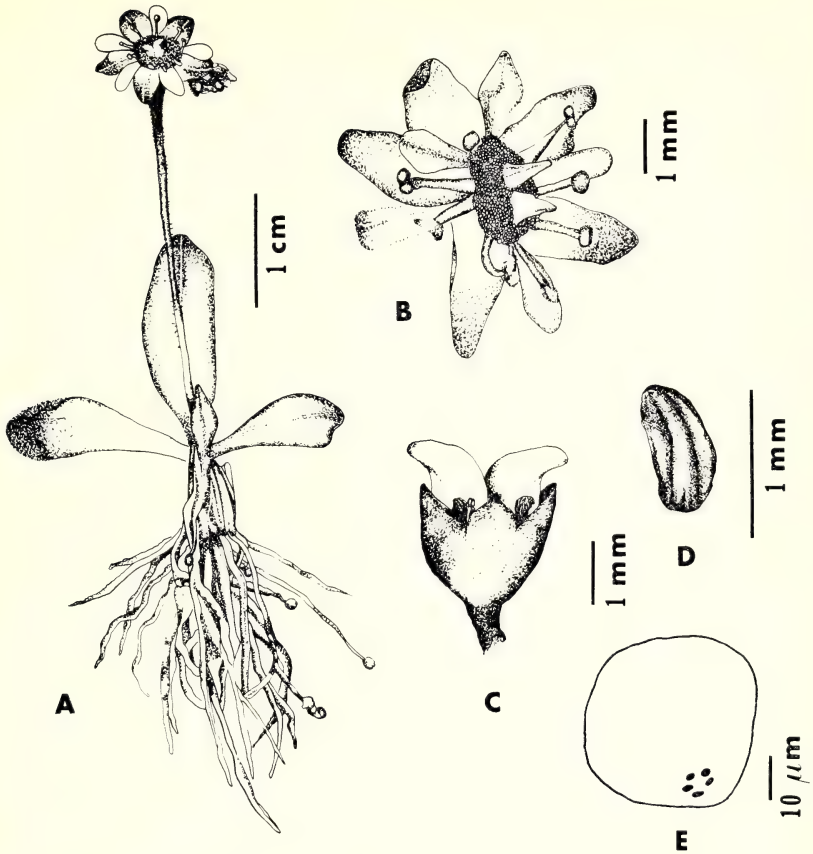

FIG. 1. *Saxifraga tempestiva*. A, habit; B, flower; C, fruit; D, seed; E, camera lucida drawing of pollen mother cell, Metaphase I; A and B drawn by Nancy Williams; C and D drawn by Carolyn Greene; all from *Elvander 440*.

HABITAT: In the Bitterroot Mountains, the plants have been found only on the north-facing slope of East St. Joseph Peak on rocky ledges under *Larix lyallii,* but in the Anacondas, they occur in open, vernally moist depression areas of alpine meadows and slopes where winter snowfall persists until late June, July, or August. The known collections are from elevations of 2400 to 3150 meters.

PHENOLOGY: Flowering specimens have been collected in June and July, and fruiting specimens in July and August.

ADDITIONAL COLLECTIONS: Montana, Deerlodge Co., Anaconda Range, about 15 mi SW of Anaconda, Little Rainbow Mt., *Lackschewitz 4531* (MONTU, WTU); Little Rainbow Mt., about 1 mi E of Storm Lake Pass, *Elvander 489* (WTU); peak of Little Rainbow Mt., ½ mi E of Storm Lake Pass, *Elvander 490* (WTU); 1½ mi toward Storm Lake

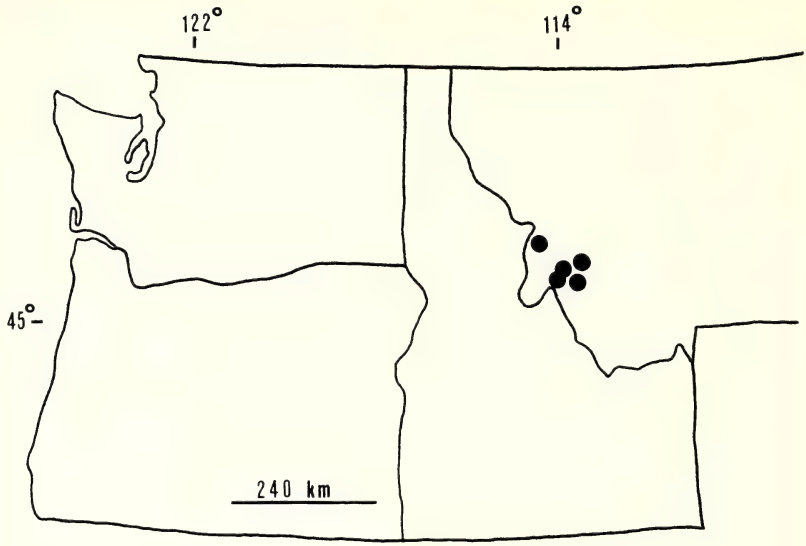

FIG. 2. Distribution of *Saxifraga tempestiva*.

Pass from Storm Lake Dam, *Elvander 438* (WTU); Goat Flat, about two-thirds mi W of Storm Lake Pass, *Elvander 440, 493* (both WTU); north slope of Mt. Tiny above Storm Lake, *Lackschewitz and Elvander 447a* (WTU); Green Mt. above Storm Lake, *Lackschewitz s.n.* (MONTU); Anaconda Range, about 25 mi SW of Phillipsburg above Big Johnson Lake, S side of Pintlar Pass, *Elvander 506* (WTU); slope of the ridge ¼ to ½ mi from Pintlar Pass toward E. Pintlar Peak, *Elvander 507, 508* (both WTU). Ravalli Co., Bitterroot Mts., E. St. Joseph Peak, *Lackschewitz 2122* (MONTU, WTU); about 25 mi S of Missoula, *Elvander 468* (WTU). Granite Co., Anaconda Range, about 25 mi SW of Phillipsburg, above Big Johnson Lake, north slope ledges between Pintlar Pass and E. Pintlar Peak, *Elvander 504* (WTU). Beaverhead Co., Anaconda Range, summit of E. Pintlar Peak, *Hitchcock and Muhlick 12875* (WTU).

MATERIALS AND METHODS

Field and herbarium studies were conducted with seven closely related taxa of *Saxifraga* (*S. integrifolia* Hook., *S. marshallii* Greene, *S. occidentalis* Wats. var. *occidentalis* and var. *idahoensis* (Piper) Hitchc., *S. oregana* Howell, *S. rhomboidea* Greene, and *S. tempestiva*. Herbarium specimens examined are at MONTU and WTU, and vouchers for cytological preparations are at WTU. Buds for cytological studies were fixed in a solution of absolute ethanol and glacial acetic acid (3:1, v:v). After fixation, this solution was replaced with 70 percent ethanol, and the buds were refrigerated until used. Chromosome counts were obtained using standard acetocarmine squash techniques.

To assist in analysis of morphological data, two computer programs were utilized: a cluster analysis program and a stepwise discriminant analysis program. Twenty-six characters (Table 1) were selected to represent the morphological profiles of each taxon, and these data were used by both programs. Fifteen individuals from each of seven taxa were analyzed. The clustering program, MINFO (Goldstein and Grigal, 1971), uses a mutual information method (Orloci, 1969); all data were scaled to a 0–1 base for equal weighting and the resulting calculations were used to construct a dendrogram reflecting degrees of relationship. Stepwise discriminant analysis (Dixon, 1970) is classificatory and ranks each character according to its usefulness in constructing a classification; the separation of individuals as calculated by this program is graphed in two dimensions using the first two canonical variables. The two programs, because they used the same data in different ways, served as objective and complementary checks of each other.

Discussion

The predominantly inferior ovary and sessile leaves with entire to dentate margins are the main features that serve to place *S. tempestiva* along with *S. oregana* and *S. integrifolia* in sect. *Boraphila* subsect. *Integrifoliae*. The closely related subsect. *Nivali-virginienses* containing *S. occidentalis, S. marshallii,* and *S. rhomboidea,* is distinguished by usually petiolate leaves with serrate to dentate margins and ovaries that are mostly superior. *Saxifraga rhomboidea,* which is intermediate between the two subsections, is presently classified in subsect. *Nivali-virginienses* (Engler and Irmscher, 1916), mostly because this subsection contains more variability than *Integrifoliae*.

One of the most diagnostic features of *S. tempestiva* is a flattened nectary disc (fig. 3, A) that is fused entirely around the carpels and covers

Table 1. Enumeration of Morphological Characters used in both Computer Analyses (MINFO and Stepwise Discriminant Analysis). Rankings of the 12 characters selected and used in Stepwise Discriminant Analysis are indicated parenthetically.

1. Density of hairs on the stem; 2. Petal length; 3. Petal length/petal width; 4. Sepal length; 5. Petal length/sepal length (11); 6. Degree of reflexion of the sepals (2); 7. Petal shape (7); 8. Filament length; 9. Filament shape (12); 10. Pedicel length; 11. Number of flowers per inflorescence; 12. Number of branches from main axis of the inflorescence; 13. Position of the ovary at anthesis (6); 14. Leaf length/leaf width (10); 15. Petiole length; 16. Degree of serration of the leaf margins; 17. Color of gland or disc surrounding the carpels (5); 18. Height of the plant (9); 19. Color of the apical cells on glandular stem hairs (4); 20. Presence/absence of yellow spots on the petals (3); 21. Structure of the nectary gland or disc (1); 22. Degree of lobing of the nectary disc; 23. Extent of emergence of the styles from the nectary disc (8); 24. Density of hairs on the leaf margins; 25. Density of hairs on the abaxial leaf surface; 26. Degree of fusion of the nectary disc around the carpels.

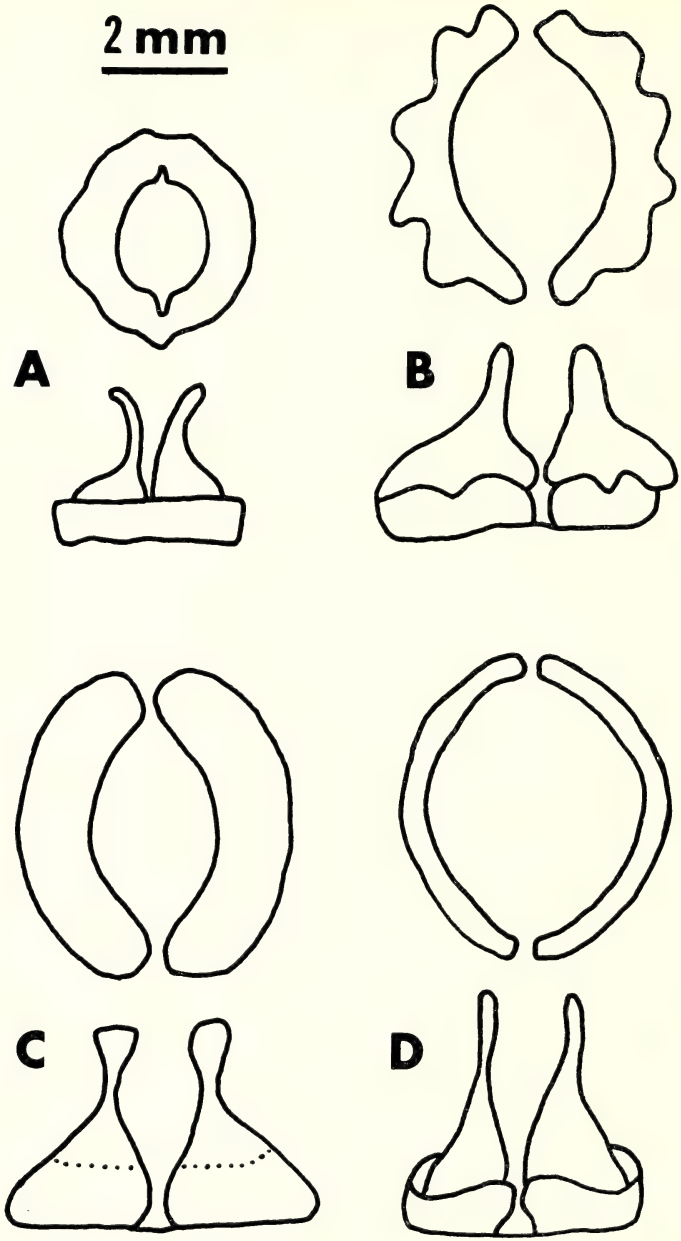

FIG. 3. Top and side views of nectary discs in *Saxifraga*. A, *S. tempestiva;* B, representative of both *S. integrifolia* and *S. oregana*; C, *S. rhomboidea*; D, *S. occidentalis*.

most of the ovuliferous portion of the ovary. The nectary discs in *S. integrifolia, S. oregana,* and *S. rhomboidea* (fig. 3, B and C) are similar to that in *S. tempestiva* because they are flattened and cover most of the ovary, but differ in that the discs are lobed, or divided in two sections, with each lobe covering a carpel. The two bandlike sections of the nectary disc in the *S. occidentalis* complex (including *S. o.* var. *o., S. o.* var. *idahoensis,* and *S. marshallii*) surround, but do not cover, each carpel (fig. 3, D).

Although *S. tempestiva* is morphologically homogeneous, the heterogeneous nature of related taxa results in intergradations that make relationships difficult to assess. Computer-assisted studies have served to clarify the relationships of *S. tempestiva* and to point out some of the taxonomic problems inherent in related taxa. Results of both the cluster analysis (fig. 4) and the discriminant analysis (fig. 5) clearly segregate *S. tempestiva* from related taxa and show agreement with subjective interpretations. In each of the programs, the *S. occidentalis* complex was separated as a group, with *S. rhomboidea* occupying a position intermediate between *S. occidentalis* (subsect. *Nivali-virginienses*) and *S. integrifolia, S. oregana,* and *S. tempestiva* (subsect. *Integrifoliae*). As an indication of the variability known for these species, all but *S. tempestiva* have had varieties and subspecies circumscribed within them (Engler and Irmscher, 1916; Kearney and Peebles, 1951; Hitchcock et al., 1961). The occurrence of apetaly and micropetaly in several of the varieties contributes to the difficulty in their identification. For example, in the results of the cluster analysis (fig. 4), the classification of two morphological forms of *S. integrifolia* is dichotomous rather than parallel; these two forms are described as "varieties *apetala* and *leptopetala*". Those specimens grouped near *S. rhomboidea* are all "var. *apetala*", while those specimens grouped near *S. oregana* are all "var. *leptopetala*". The computer analysis does not recognize a discrete taxon, *S. integrifolia.* The dilemma is biological, not an artifact of the analysis, and recurs in the evaluation of other species (Hitchcock et al., 1961; Krause and Beamish, 1972, 1973; Elvander, 1975).

The meiotic haploid number of five for *S. tempestiva* (fig. 1) provides a new chromosome number for *Saxifraga* as well as for the Saxifragaceae. The low haploid numbers reported for *Saxifraga* are $n = 7, 8, 9, 10, 11, 12, 13, 14,$ and 15, to which 5 can now be added. The haploid number of 6 is not yet reported, but only about 30 percent of the estimated 325 species of *Saxifraga* have been investigated cytologically. Available haploid chromosome numbers for taxa of *Saxifraga* in subsects. *Integrifoliae* and *Nivali-virginienses* occurring in the Pacific Northwest range from 10 to 60 (cited in standard indices). Although numerous aneuploid and polyploid derivatives limit establishment of relationships among taxa on chromosomal evidence, the chromosome number of five may be the original basic number from which the chromosome numbers in *S. rhom-*

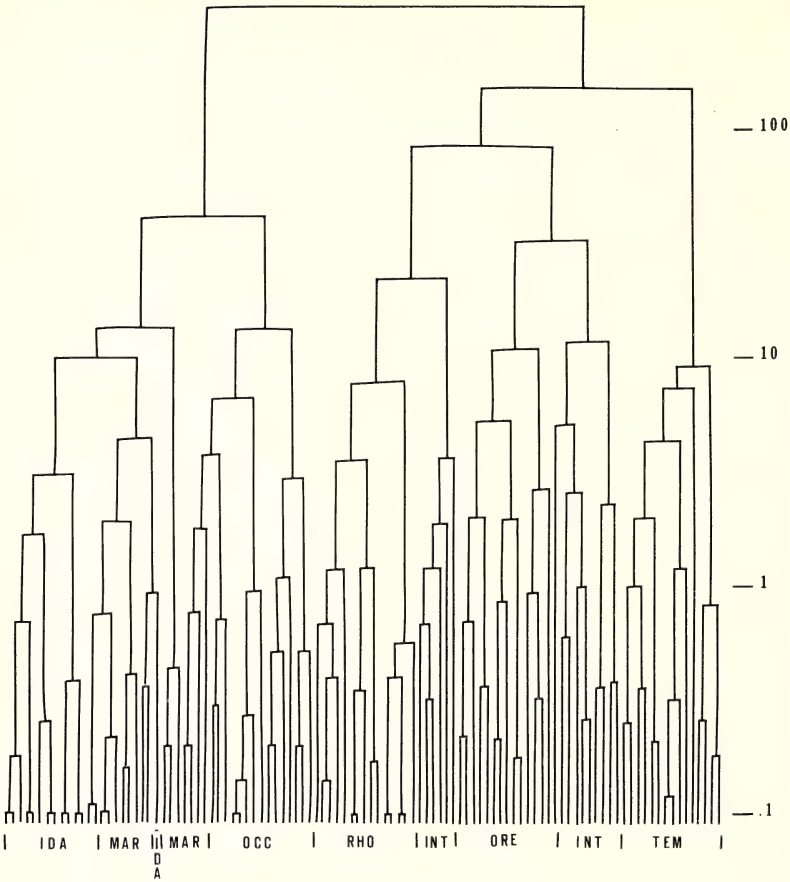

FIG. 4. Dendrogram reflecting degrees of relationship among individuals of each taxon used in the cluster analysis program (MINFO). IDA, *S. occidentalis* var. *idahoensis*; MAR, *S. marshallii*; OCC, *S. occidentalis* var. *o.*; RHO, *S. rhomboidea*; INT, *S. integrifolia*; ORE, *S. oregana*; TEM, *S. tempestiva*. The vertical scale is logarithmic.

boidea, S. occidentalis complex, *S. oregana,* and *S. integrifolia* were derived. *Saxifraga tempestiva* could be a relict species maintaining an ancestral number of five or be a product of reversible tetraploidy (Raven and Thompson, 1964; De Wet, 1971). The well-defined habitat, mostly inferior ovary, and nectary disc of *S. tempestiva* suggest that it is a specialized species and not ancestral to the other species in subsect. *Integrifoliae* or to those in subsect. *Nivali-virginienses.*

ACKNOWLEDGMENTS

Support for this research was provided by a grant-in-aid of research from the Society of Sigma Xi to P. Elvander and by the Department of

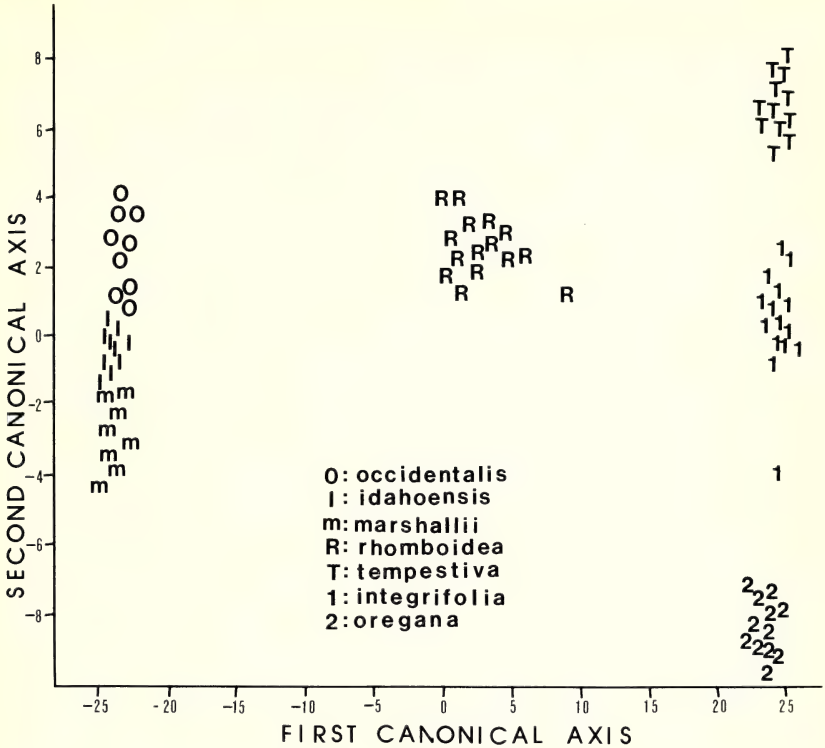

FIG. 5. Distribution of the taxa in canonical space (Stepwise Discriminant Analysis). The first two axes account for 97.4 percent of the variation exhibited by the individuals used in the analysis.

Botany, University of Washington. We are grateful to K. Lackschewitz for field assistance, to D. E. Stuntz for editing our Latin description, and to R. del Moral and A. R. Kruckeberg for their advice during the study.

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A NEW SUBSPECIES OF RHUS CHONDROLOMA (ANACARDIACEAE) FROM MEXICO

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During my biosystematic investigation of *Rhus* subg. *Lobadium* (Young, 1975), a new subspecies of *Rhus chondroloma* Standley was discovered. Because the new subspecies and *R. chondroloma* ssp. *chondroloma* are involved in hybrid complexes with *Rhus standleyi* Barkley it is desirable to publish the description of this new taxon before the details of hybridization are presented.

Rhus chondroloma Standley ssp. **huajuapanensis** Young, ssp. nov. (fig. 1). A ssp. *chondroloma* differt: rami et petioli et segmenta rachidis et foliola pubescentes; foliola parviora et numerosiora.

Type: Mexico, Oaxaca, distrito Huajuapan, ca 2 mi N of Huajuapan de Leon, on limestone palm lands along Mex Hwy 190, ca 1620 m, 22 Jan 1974, *S. L. Buchmann and D. A. Young 1–96*. Holotype: RSA; isotypes: MEXU, TEX, UC, US.

Aromatic evergreen shrub or small tree 1–6 m high, with relatively stout, brownish, densely pubescent twigs, dotted with reddish lenticels. Leaves pinnately compound, 3–9 leaflets (most frequently 7), 7.0–10.0 (8.5; numbers in parentheses are the mean for a particular character) cm long; leaflets coriaceous, entire, slightly revolute, margin white-corneous, conspicously pallid-veined, bluish-green above, pale green below; terminal leaflet 2.0–4.0 (3.0) cm long, 1.5–4.0 (2.5) cm wide, distinctly obovate, apex obtuse to rounded (rarely retuse to emarginate), base obtuse; lateral leaflets 2.0–4.0 (3.0) cm long, 1.5–2.5 (1.7) cm wide, elliptic to oval, obtuse at both ends, sessile to subsessile; upper surface of leaflets pilose to puberulous, veins densely pubescent, margins ciliate, lower surface pilose, also densely covered with sessile orange-glandular trichomes. Petioles 1.0–3.0 (1.9) cm long, wingless; rachis segments 1.0–2.5 (1.8) cm long, distinctly winged; petioles and rachis

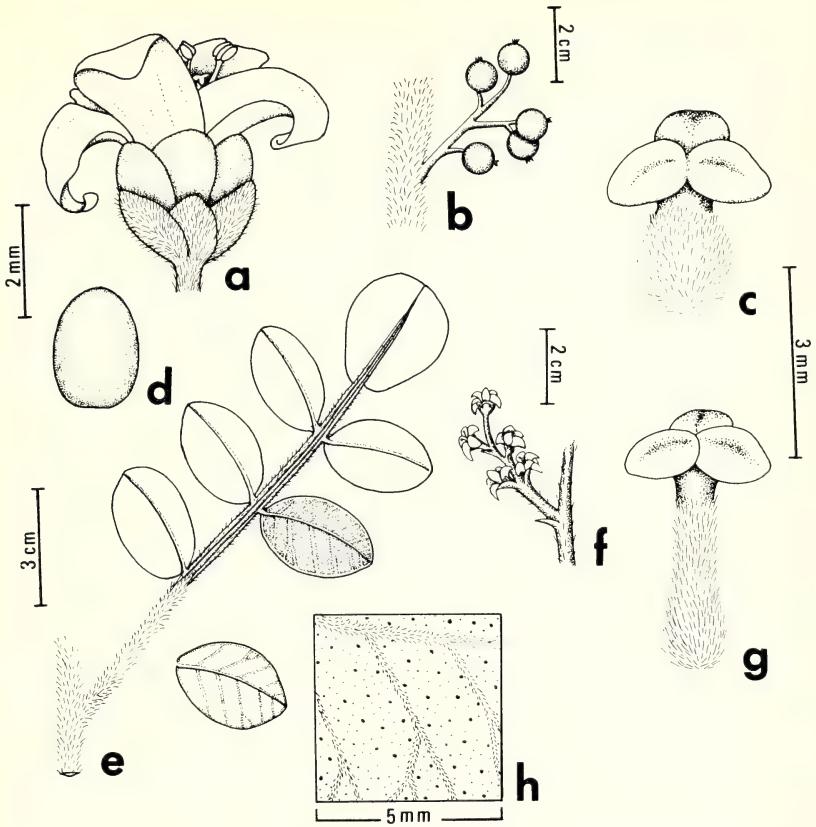

FIG. 1. *Rhus chondroloma* ssp. *huajuapanensis*. a, male flower; b, fruits; c, pistil of female flower; d, sepal; e, leaf; f, inflorescence; g, pistil of male flower; h, lower surface of leaflet (dark dots represent glandular trichomes).

segments covered with a dense soft pubescence. Inflorescences small, dense, terminal spikes, ca 1–4 cm long, slightly narrower. Bracts ovate-deltoid, ca 1–2 mm long, 1.5–2.0 mm wide, densely pubescent on outer surface with simple and orange-glandular trichomes, glabrous on inner surfaces. Sepals greenish-pink, rotund, ca 1–2 mm in diameter, sparingly ciliate with simple and orange-glandular trichomes. Petals white, oval, sexually dimorphic (smaller in male-sterile flowers), ca 2.5–4.0 (3.4) mm long, ca 1.5–2.5 (2.0) mm wide, glabrous, not ciliate. Stamens smaller than sepals in male-sterile flowers, slightly longer than sepals in hermaphrodites. Styles 3, more or less distinct. Fruit a drupe, pubescent with reddish-orange glandular trichomes and long simple trichomes, ca 8–10 mm in diameter.

HABITAT AND DISTRIBUTION (fig. 2): Endemic to the limestone soils in the area surrounding Huajuapan de Leon, Oaxaca, and adjacent Puebla,

Mexico. Some common associates are: *Amelanchier denticulata, Tecoma stans, Lippia* spp., *Mimosa* spp., and *Ptelea trifoliolata.*

SPECIMENS EXAMINED: Mexico, Oaxaca, Entre Los Cerros Jicota y Amarillo, 2300 m, *Cabrera 32* (ENCB); between Tlaxiaco and Teposcolula, *Camp 2320* (ENCB, NY); Cerro Solo, 7 km al NE de Tepeleme, 2350 m, *Cruz Cisneros 2108* (ENCB, DS, MICH, MSC); in limy soil of xeric hillside in palm land ca 8 mi N of Huajuapan de Leon, *Rowell, Webster, and Barkley 17M579* (male) and *17M580* (female) (ARIZ, ENCB, MICH, MSC, TEX, UC); Magdalena Jicotlan, distrito de Coixtlahuaca, 2100 m, *Rzedowski 26688* (DS, ENCB, MICH, MSC); on limestone 6 mi NW of Huajuapan de Leon, 6200 ft, *Webster, Miller, and Miller 11436* (MEXU, GH). Puebla, limestone hills with shrubby vegetation, Mex Hwy 125, 0.9 mi NE of Acatepec, *Denton 1485* (MICH); Chila, hillslope, *Saunder s.n.* (ENCB).

Key to subspecies of *Rhus chondroloma*

a. Leaflets mostly trifoliolate (1–7), often unifoliolate, glabrous; terminal leaflet 4.5–6.5 cm long, 2.5–5.0 cm wide, lateral leaflets 2.5–4.5 cm long, 1.5–3.0 cm wide; petioles and rachis segments glabrous; Guerrero and Puebla. . . . . *R. chondroloma* ssp. *chondroloma*

aa. Leaflets mostly 7 (3–9), pubescent; terminal leaflet 3.0–4.0 cm long, 1.5–4.0 cm wide; lateral leaflets 2.0–4.0 cm long, 1.5–2.5 cm wide; branches, petioles and rachis segments pubescent; Oaxaca. . . . . *R. chondroloma* ssp. *huajuapanensis*

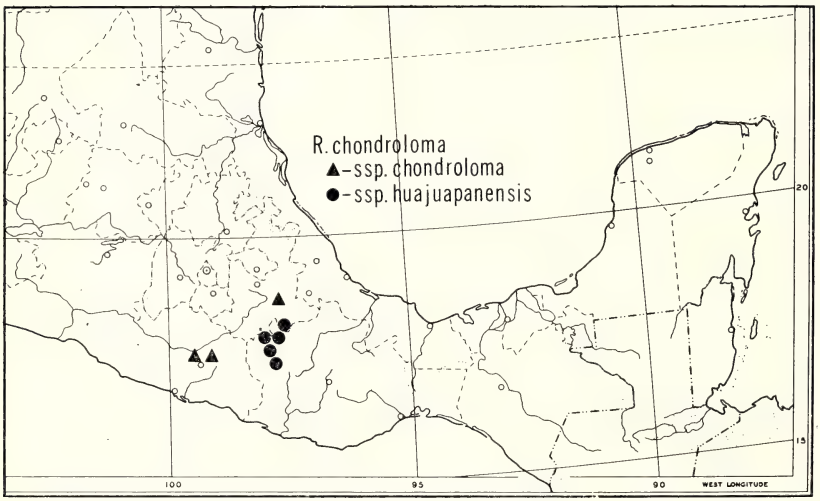

FIG. 2. Geographical distribution of the two subspecies of *Rhus chondroloma.* (Base map used by permission of the editor of Goode Base Maps, copyright by The University of Chicago Department of Geography).

Rhus chondroloma ssp. *huajuapanensis* differs most noticeably from *R. c.* ssp. *chondroloma* (Standley, 1936) in its markedly pubescent branches, petioles, rachis segments, and leaflets and in its smaller, more numerous leaflets. *Rhus c.* ssp. *huajuapanensis* appears to flower mainly from May to July, although a few flowers were present on one herbarium specimen examined collected in January. My collections in January were all in bud; mature fruits were present in September. The species is subdioecious; morphologically bisexual flowers were present, but either the anthers or ovules appeared to be nonfunctional. No pollinators were observed.

In the herbarium material examined, this subspecies was consistently identified as *Rhus duckerae* Barkley, and it keys to *R. duckerae* in Barkley's (1937) key. *Rhus c.* ssp. *huajuapanensis* is quite distinct from the type of *R. duckerae* (US!), which is the only collection of the latter taxon. The status of *R. duckerae* as a distinct species is questionable. Preliminary studies suggest that *R. duckerae* is actually a hybrid between *R. oaxacana* Loesen. and *R. standleyi* (Young, 1975).

Acknowledgments

I thank Drs. S. Carlquist, C. E. Jones, R. Scogin, and R. F. Thorne for critically reading the manuscript, which represents a portion of my Ph.D. Dissertation submitted to the Claremont Graduate School, Claremont, California. Field studies were supported by National Science Foundation grant (Improving Doctoral Dissertations in the Field Sciences) GB 38327. Thanks are also due to Consejo Nacional de Ciencia y Tecnologia, Mexico City, Mexico, for a collecting permit (No. 1/609–5466), the Editors of the Goode Base Maps for permission to use their copyrighted base map, Susan Payne for Figure 1, and the curators of the following herbaria for loans of specimens: ARIZ, DS, ENCB, GH, MEXU, MICH, MSC, NY, TEX, UC, US.

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CHRYSANTHELLUM PILZII (COMPOSITAE), A NEW SPECIES FROM OAXACA

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Botany – Herbarium, University of California, Berkeley 94720

Curating can be rewarding. I first noticed the following, heretofore undescribed, taxon as a single, unidentified specimen in UC (Oaxaca, Salina Cruz, 15 Jul 1946, *T. Morley 680*). George Pilz and I went to Oaxaca to collect the "new" taxon. He found it before I did. I am naming it for him in recognition of his prowess.

Chrysanthellum pilzii Strother, sp. nov. A ceteris *Chrysanthellis* combinatione foliorum caulinorum oppositorum, flosculorum discorum fungenter staminatorum, acheniorum circinatorum et aculeotorum differt. Figure 1.

Type: Mexico, Oaxaca, ca 1 km east of Salina Cruz (ca 16°12′N, 95°09′W), beach sand, 22 Jul 1971, *Strother 1094*. Holotype, UC; isotypes to be distributed to K, MEXU, MICH, TEX, US.

Prostrate to ascending annuals; stems several, mostly 5–15 cm long, terete, striate, sparsely hirsute to glabrescent. Basal leaves mostly 4–10 cm long including petioles 2–6 cm long; cauline leaves opposite, smaller; blades 1–2 pinnatisect, lobes cuneate to lanceolate, ultimate divisions often toothed, upper surfaces green, sparsely pubescent with short, erect, simple hairs and scattered, gland-tipped hairs, lower surfaces whitish, glabrous or nearly so, covered with thick, opaque cuticle. Heads solitary at ends of branches, borne on erect, naked peduncles 2–10 cm long. Involucres turbinate to campanulate. Phyllaries mostly 8, imbricate, graduate, lanceolate to ovate, 4–6 mm long, purplish, striate, scarious-margined, subtended by 3–5 short, lanceolate bractlets. Receptables slightly convex, paleaceous; paleae 3–5 mm long, very slender, scarious-margined. Ray florets pistillate, fertile, mostly 8(–12); corollas ligulate, golden yellow with darker nerves, tube ca 0.5 mm long, lamina ovate-elliptic, retuse, 4.5–5.5 mm long; style branches 0.4 mm long, minutely papillate, stigmatic; achenes 5–6 mm high, circinately recurved, adaxial surface convex, purplish, prickly, abaxial surfaces concave, stramineous, smooth; pappus none. Disc florets functionally staminate, mostly 40–50; corollas dark yellow, distally tinged with purple, 3.0–3.5 mm long, tube cylindric, ca 1 mm long, throat campanulate, ca 2 mm long, lobes 5, deltoid, erect, ca 0.5 mm long; style branches ca 2 mm long, papillate-hirtellous throughout, nonstigmatic; anthers 5, ca 1.5 mm long including blunt apical appendages and short basal collars; ovaries elongating to ca 3 mm but not forming achenes.

Chrysanthellum comprises about a half dozen species of diminutive annuals that grow in mostly subxeric habitats in Old and New World tropics and subtropics. Some are apparently weedy.

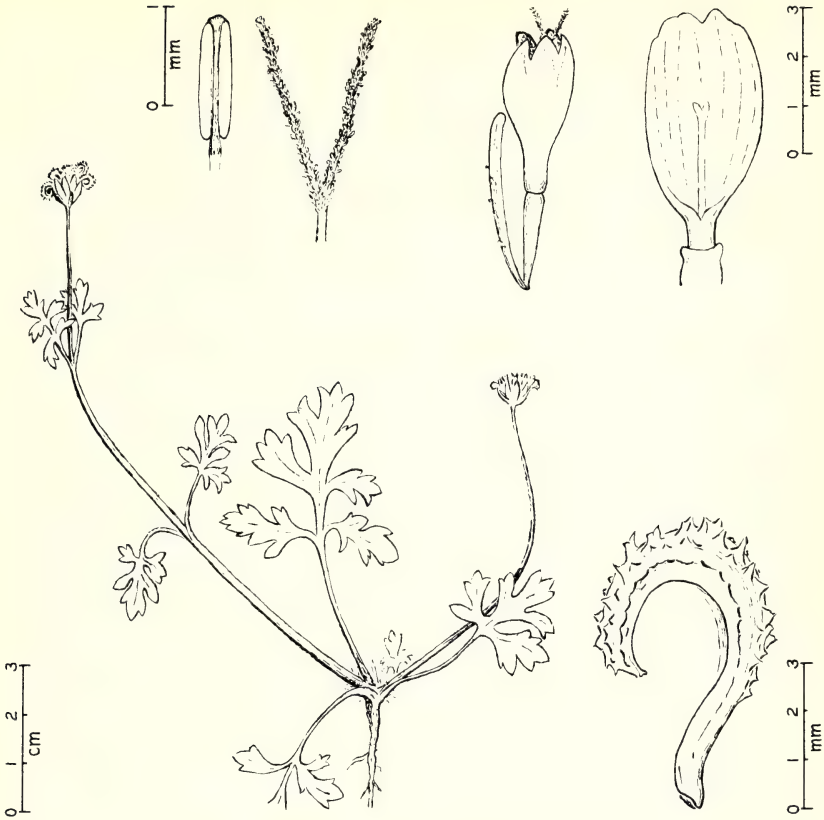

FIG. 1. Habit and details of *Chrysanthellum pilzii*. All from type collection.

Smith and Turner (1975) surveyed numerous Compositae for Kranz syndrome (C_4 photosynthetic metabolism). All Chrysanthellums that they examined (four species) were found to be Kranz plants as were representatives of *Eryngiophyllum, Glossocardia, Glossogyne,* and *Isostigma* (all Coreopsidinae). Turner (in Smith and Turner, 1975) indicated that these genera, including *Chrysanthellum,* also form "a natural group" morphologically. Leaf anatomy of *C. pilzii* suggests that it too is a Kranz plant.

Chromosome numbers for Chrysanthellums are: *C. mexicanum* Greenm., $n = 8$ (DeJong and Longpre, 1963; Powell and Turner, 1963); *C. involutum* P. G. Wilson, $2n = 8$ II (Strother, 1972); and *C. pilzii,* $2n = 12$ II (reported here from type collection). The relationship of the 12 to the 8's is puzzling; sound speculation cannot be offered without additional information.

Reproductive biology in *Chrysanthellum* also merits investigation. In widespread, weedy taxa [e.g., *C. americanum* (L.) Vatke and *C. indicum* DC.], there is often a tendency for disc florets to be functionally staminate. In more narrowly distributed taxa (*C. filiforme* McVaugh, *C. involutum,* and *C. pilzii*), disc florets apparently never set achenes.

Field work was supported in part by a grant (GB-7995) from National Science Foundation.

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NOTES AND NEWS

George W. Gillett, 1917–1976.—Professor Gillett died on 14 Jan 1976 at Loma Linda, following open-heart surgery. He was born in Clifton Springs, New York, on 30 May 1917 and grew up in Carroll, Iowa. He received a B.S. in Forestry at Iowa State University in 1940 and served with the U. S. Air Force and worked for the U. S. Forest Service before earning a M.F. at University of California, Berkeley, in 1949. He went on to earn a Ph.D. in botany at Berkeley in 1954. He taught at Bakersfield College, Michigan State University, University of Hawaii, and University of California, Riverside. George Gillett was known widely through the world for his detailed taxonomic studies in such genera as *Cyrtandra, Bidens, Scaevola, Wikstroemia,* and *Pipturus* and for his interest in Pacific biogeography. His earlier interests included *Phacelia* and the flora of Lassen National Park. A careful planner, George was completing arrangements for an extensive *Cyrtandra* collecting trip to interior New Guinea only a few days before his death. His many friends esteemed him as a competent, thorough taxonomist and as a colleague and scientist of very high standards. Mostly, however, he will be remembered as a good friend whose many thoughtful courtesies evoke the reflection that he took time to be a gentleman.

Agrostis thurberiana (Gramineae), New to Southern California.—*Agrostis thurberiana* Hitchc. has been collected: San Bernardino Co., South Fork of Santa Ana River, San Bernardino Mts., N slope, wet sandy soil in shaded meadow in Yellow Pine Forest, ca 2400 m, 1 Aug 1974, *Gordon et al. 518* (SFV).

The previously acknowledged range of *A. thurberiana* extends southward from British Columbia to the North Coast Ranges of Humboldt County and in the Sierra Nevada to Tulare County (Munz, *A California flora,* 1959). It also occurs in the Rocky Mountain region south to Utah and Colorado (Hitchcock and Chase, *Manual of the grasses of the United States,* 1950).

Many characteristically northern plants have southern outposts in the San Bernardino Mountains, e. g., *Bromus ciliatus* L. and *Festuca rubra* L., both of which were found growing in close association with *A. thurberiana* at the Santa Ana River site.—Michael H. Grayum and Thomas R. Gordon, Biology, California State University, Northridge 91324.

Montana Mountain Flora: New Records.—As a result of intensive botanical exploration in the Bitterroot Mountains, Missoula and Ravalli Counties, in the mountains of the Anaconda-Pintlar Wilderness area along the Continental Divide, Deer Lodge and Granite Counties, further collecting to the north on Choteau Mountain, Teton County, and to the east in the Bridger Mountains, Gallatin County, as

well as study of specimens in MONTU, eleven new records for Montana, two additional range extensions, and collections confirming two previously undocumented records for the state are reported here. Previously known distributions and nomenclature are those given in Hitchcock and Cronquist (*Flora of the Pacific Northwest,* 1973) unless otherwise indicated. Collections were made by the author and are deposited in MONTU and other herbaria as indicated. Identifications were either made or verified by A. Cronquist, F. J. Hermann, C. L. Hitchcock, or W. H. Wagner, Jr. L. H. Harvey helped in editing the manuscript.

New Records

Selaginella selaginoides (L.) Link. Deer Lodge Co., Sec 30 T4N, R13W, SW of Storm Lake on lower east slope of Mt. Tiny, 2538 m, 19 Jul 1973, *4552*; 3 Sep 1974, *5783*. Granite Co., Sec 5, T2N, R15W, Johnson Lake, 2330 m, 25 Sep 1974, *5899,* NY, WTU.

Polystichum kruckebergii Wagner. Deer Lodge Co., Sec 36, T4N, R14W, S slope of Mt. Tiny, 2840 m, 10 Sep 1971, *4111,* MTMG, NY, MTU; in an identical habitat circa 70 m W of above, 4 Sep 1974, *5793,* COLO, WTU.

Polystichum scopulinum (D. C. Eaton) Maxon. Ravalli Co., Sec. 28, T10N R21W, S slope of St. Joseph Peak, 2196 m, 24 Jul 1971, *2963,* NY. A much more typical plant of this species, much larger, with deeply incised pinnae was collected 0.25 km SW above Walton Lakes, in the Clearwater National Forest, Idaho Co., Idaho (Sec 28, T36N, R15E), 5 Aug 1972, *3899,* MTMG, NY, WTU.

Luzula arcuata (Wahlenb.) Wahlenb. Glacier Co., Logan Pass, Glacier National Park, 2275 m, 7 Aug 1964, *Harvey and Pemble 7096.* Missoula Co., Sec 28, T11N, R21W, N slope of Lolo Peak, Bitterroot Mts., 2713 m, 8 Sep 1968, *Lackschewitz and Fageraas 1065.* Ravalli Co., Sec 25, T32N, R23W, N slope of White Mt. in Lost Horse Creek Drainage, 2640 m, 10 Aug 1970, *2247,* USFS; Sec 8, T30N, R22W, E slope of "Bedrock Mountain", southwest of Chaffin Lake, 2745 m, 7 Aug 1971, *3194,* NY, USFS, WTU; Sec 4, T30N, R22W, N slope of Chaffin Peak, 2835 m, 30 Aug 1971, *3412,* WTU; Sec 3, T20N, R22W, below N slope of Sugarloaf Peak S of Hart Lake, 2530 m, 31 Aug 1971, *3462.* In this same general area three Pacific Northwest species (*Anemone occidentalis, Luetkea pectinata,* and *Romanzoffia sitchensis*) are believed to reach their southernmost distributional limits in Montana.

Carex incurviformis Mack. var. *danaensis* (Stacey) F. J. Hermann. Deer Lodge Co., Sec 31, T4N, R13W, NE slope of "Little Rainbow Mt.", SW above Storm Lake, 2699 m, 31 Aug 1972, *3938,* NY, USFS.

Carex petricosa Dewey. Glacier Co., NW slope of ridge near timberline, Divide Mt., 2175 m, 9 Aug 1964, *Harvey and Pemble 7182;* on windswept ridges in *Dryas* mats, Divide Mt., 2190 m, 14 Aug 1964, *Harvey and Pemble 121.*

Carex praeceptorum Mack. Missoula Co., Sec 27, T11N, R21W, E slope of Lolo Peak above Carlton Lake, 2470 m, 5 Sep 1971, *Lackschewitz and Stickney 3483,* USFS.

Eriogonum umbellatum Torr. var. *stellatum* (Benth.) Jones. Ravalli Co., Darby, 11 Jul 1924, *Kirkwood 2092;* Sec 17, T28N, R23M, S slope above Sheephead Creek, 1616 m, 4 Jul 1974, *Jaculyn Cory 1153.* All known Montana localities are on the E slope of the Bitterroot Mts. within a distance of 50 km.

Lesquerella carinata Rollins. Granite Co., Sec 26 T6N, R16W, on W slope and crest of ridges, N of Hwy. 38 and E of road to Richtmeyer Ranch, E foothills of the Sapphire Range, 1660 m, 24 June 1972, *3688,* NY, WTU.

Pyrola elliptica Nutt. Ravalli Co., Sec 36, T9N, R21W, near St. Mary's Rd. ca. 2 miles W of US 93, 1098 m, 5 July 1974, *5151,* WTU; from almost same locality, 10 July 1974, *5166,* COLO, NY; Sec 11, T5N, R21W, Cory place, SW of Hamilton, 1110 m, 24 July 1974, *Jaculyn Cory 1176.* In both localities several well-developed colonies were found. They are 22 km apart. Rydberg (Mem. New York Bot. Gard. 1:492. 1900) cited a collection from Montana: Highwood Canyon, 1889, *R. E. Williams 839.* This is in the Highwood Mts., 50 km E of Great Falls. That area is

not covered by Hitchcock and Cronquist (op. cit.) and no reference to that species by any authors subsequent to Rydberg could be found.

Saussurea weberi Hulten. Deer Lodge Co., Sec 36, T4N, R14W, upper W slope of Goat Flats, 2790–2840 m, 28 July 1973, *4583,* COLO, MTMG, NY, WTU; same locality, common on SW facing slope, 12 Aug 1973; *Witherspoon and Schaack 8218,* COLO, *Witherspoon 8222;* SW facing sloope, *Schaack and Witherspoon 881,* COLO; SW slope, *Schaack and Witherspoon 883,* COLO.

Range Extensions

Pellaea breweri D. C. Eat. Teton Co., Sec 11, T25N, R9W, W slope of Choteau Mt., 2045 m, 28 May 1973, *4285,* NY. This locality is 120 km S of the Canadian border and 13 km E of the Continental Divide. Gallatin Co., Sec 25, T1N, R6, E ridge of the Bridger Mts., near Bridger Bowl Ski Area, 2440 m, 12 July 1974, *5185,* NY, WTU. Deer Lodge Co., Sec 26, T4N, R14W, S slope of Mt. Tiny, 2837 m, 4 Sept 1974, *5792,* COLO, NY, WTU. This fern is probably not as rare as formerly assumed and probably occurs along the Continental Divide to some point south of Glacier Park. Specimens cited here extend the known range 350 km N.

Salix dodgeana Rydb. Bamberg and Major (Ecol. Mongr. 38:127–168. 1968) report it from Flint Creek Mts., Granite Co. The latter is the only previously known station W of the Continental Divide. Deer Lodge Co., Sec 32, T4N, R13W, N slope of Little Rainbow Mt., 2989 m, 2 July 1972, *3769;* Sec 31, T4N, R13W, NE slope of Little Rainbow Mt., 2699 m, 13 Aug 1972, *3942,* NY; Sec 1, T3N, R14W, Goat Flat below Kurt Peak, 2882 m, 28 July 1973; Sec 6, T2N, R14W, E slope of Goat Peak above Lost Lakes, 2938 m, 21 Aug 1973, *4723,* MTMG, NY, WTU. Teton Co., Sec 12, T25N, R9W, W slope of Choteau Mt., East Front Mts., 2440 m, 7 July 1973, *4424,* MTMG, NY, WTU. These collections extend its known range 210 km N.

Range Verifications

Carex breweri Bott. var. *paddoensis* (Suksd.) Cronq. Missoula Co., Vacation Pass, Mission Mts., 2684–2745 m, 11 Aug 1968, *Stickney 1715,* USFS; NE head of Albino Basin, Swan Range, 2440 m, 22 Aug 1970, *Stickney 2213,* USFS; Holland Peak, Swan Range, 2715 m, 14 Aug 1970, *Arno 1002;* Holland Peak, 2684 m, 14 Aug 1970, *Arno 1020.* Ravalli Co., saddle E of St. Joseph Peak, Bitterroot Mts., 2867 m, 24 July 1971, *2989,* MTMG, WTU; Trapper Peak, 2958 m, 10 Sep 1970, *2605,* USFS; Ward Mt., 2730 m, 25 Aug 1970, *2465,* COLO, MTMG, NY, USFS. Deer Lodge Co., above Lost Lakes, E cirque of Goat Peaks, 2897–3050 m, 21 Aug 1973, *4667,* COLO, and *4704,* NY; cirque NE of Goat Peaks, 2890–3019 m, 23 Aug 1974, *5667,* WTU. Hitchcock and Cronquist (op. cit.) stated "reputedly Montana".

Carex rupestris Allioni. Hermann (USDA For. Serv. Agric. Handbook, 1970) includes Montana in the outlined distribution pattern but doesn't mention it explicitly. Bamberg and Major (op. cit.) report it from Glacier Park, the Big Snowy Mts., and the Flint Creek Mts. Teton Co., Choteau Mt., 2440 m, 7 July 1973, *4426,* NY. Missoula Co., Holland Peak, Swan Mts., 2684 m, 14 Aug 1971, *Arno 1015;* One Horse Ridge, Lolo Peak, Bitterroot Mts., 2477 m, 11 July 1970, *2136.* Ravalli Co., Sweeney Peak, 2775 m, 28 July 1969, *2008,* NY, USFS; St. Joseph Peak, 2628–2715 m, 29 Aug 1970, *2512;* saddle of St. Joseph Peak, 2867 m, 24 July 1971, *2985,* WTU; St. Mary's Peak, 2836 m, Aug 1968, *Arno 180.* Deer Lodge Co., Green Mt., E of Storm Lake, 2097 m, 4 Aug 1973, *4642,* MTMG, USFS; Goat Flats, just N of Kurt Peak, 2906 m, 10 Sep 1972, *4122;* N above Lost Lakes, E slope of Goat Peaks, 2927 m, 21 Aug 1973, *4719;* summit of Pagoda Mt., 0.5 km E of Pintlar Pass, 2867 m, 28 July 1974, *5451.* Hitchcock and Cronquist (op. cit.) stated "to be expected in Montana".—Klaus H. Lackschewitz, Department of Botany, University of Montana, Missoula 59801.

REVIEWS

A field guide to the common and interesting plants of Baja California. By Jeanette Coyle and Norman C. Roberts. xi + 206 pp., 189 color photographs, drawings, 2 maps. Natural History Publishing Co., P. O. Box 962, La Jolla, California. 1975. Hardbound, $11.00; paper, $8.50.

With the opening of the transpeninsular highway, more and more Gringo tourists are travelling through Baja California and seeing strange and intriguing plants. For the botany of desert parts of the peninsula, there is an excellent technical account, Shreve and Wiggins' *Vegetation and flora of the Sonoran Desert* (Stanford Univ. Press, 1964); but a need has now arisen for popular books for the average traveler. Besides the book under review, one other helps fill this need. *The Boojum and its home* by Robert R. Humphrey (Univ. Arizona Press, 1974) is mainly an account of one tree, the plant wonder most likely to arouse the curiosity of every traveler, known to natives as Cirio, to some Gringos as Boojum, and to botanists as *Fouquieria* (or *Idria*) *columnaris*. However, this book also tells much about Baja California in general and the central desert and its plants in particular. Coyle and Roberts' book, though less competent botanically, gives much broader coverage and so will better serve those who want just one book to tell them about more different plants.

The introduction briefly discusses the physical setting, climate, geology (by Dr. Richard P. Phillips), phytogeographic regions, endemism, and origins of the flora. The rough map of phytogeographic areas shows several areas of "Mountain Forest" scattered the length of the peninsula, for which no explanation appears in the text; these are in no sense one phytogeographic area. Next comes a key to those families represented in the book—a key clearly extracted, without acknowledgment, from Shreve and Wiggins. The "Family List" that follows is a table of contents without page numbers; spread over 11 pages, it is filler serving no obvious purpose. The "Phytogeographic Lists" might better have been incorporated into the discussion of phytogeographic regions. Illustrations of botanical terms are sketchy and drawn without understanding, and some are misleading. At the back of the book are a glossary of botanical terms and Spanish words, a bibliography, and the usual index.

The reason for the family key is not clear. Most users of the book will be non-botanists, who will find plants by thumbing through and looking at pictures; this technical key, including undefined terms and having no explanation of its use, will do nothing for them. And if *they* don't really need the key, why should a botanist? He probably will prefer the easy way like everyone else rather than keying the plant just to show he knows how. (If he should prefer to use the key, the wary botanist may first check the pictures to be sure his plant is in the book.) For plants not in the book, a key to *some* families is more frustrating than useful.

The main part of the book, 138 pages worth, is an account of the 181 plants illustrated in color, with briefer mention of 74 more. Plates and text are conveniently placed on facing pages. For each plant are given the scientific name, the family name, the English and Spanish common names, if known. A short description follows, with a statement of range and flowering time. Then, very commonly, there is information about uses and other points of interest—which is one of the best features of the book.

The book includes some plants that the traveler down the main highway will not see, such as conifers of the northern mountains. The decision of what plants to include doubtless was influenced by what pictures were available; some of these were not taken in Baja California. *Opuntia basilaris,* if it occurs there at all, would never be voted the prickly pear most likely to be encountered by the casual visitor: at least I, as a less casual visitor, have yet to see it. Generally speaking, however, the selection of plants seems reasonably good.

The photographs are mostly about 3 by 3¼ inches and arranged three to a page. Most are good, though a few are too dark, and most will help greatly in identifying plants. However, eight are not identified to species, and several appear to be misidentified. Most of the photographs were taken by non-botanists, who did not bring back specimens for checking, and sometimes identification of pictures is difficult. For anyone wanting another view of some identifications, I list mine here with page number and "U", "M", or "L", for upper, middle, or lower: 45L, *Typha latifolia*; 53L, *Juncus acutus*; 55U, *Nolina bigelovii*; 73L, *Abronia* × *platyphylla*; 75L, *Romneya coulteri*; 79U, *Dudleya pulverulenta*; 79M, *Dudleya attenuata*; 97U,

Astragalus douglasii; 101U, *Lupinus succulentus*; 103U, *Krameria grayi*; 115L, *Bursera microphylla*; 135M, *Ferocactus acanthodes*; 135L, *Ferocactus peninsulae*; 143L, *Opuntia basilaris*; 145U, *Lemaireocereus thurberi*; 149U, *Arctostaphylos pungens*; 149M, *Limonium perezii* (not the native species but a Canary Island plant grown and sometimes escaping in southern California); 153L, *Eriodictyon lanatum*; 157L, *Datura wrightii*; 159U, *Lycium* sp., not *L. californicum*; 161U, *Castilleja affinis*; 175M, *Amauria rotundifolia*; 175L, *Helianthus gracilentus*.

The text is inaccurate in many details. For example, elevations for various northern plants, evidently taken from California floras, are not correct for Baja California—where the same plants commonly occur higher. Thus in Baja California the Sugar Pine seldom straggles below 1800m (6000 ft) and certainly never down to 600m (2000 ft.). Also the book needs more editing and is marred by more than the usual number of typhogarpicxl erors, especially in plant names.

This is the first of a projected series of nature guides from a publishing company established for the purpose. It sets a good standard for quality of color illustrations and general appearance of the book. However, there should be more emphasis on quality of text.—Reid Moran, Natural History Museum, San Diego, California 92112.

The grasses of Texas. By Frank W. Gould. 653 pp. + viii, 330 figs. Texas A & M University Press, College Station, Texas. 1975. $20.00.

The very richness of the Texas grass flora alone makes the appearance of Frank Gould's latest book of major importance to students of the family. About two-thirds of the genera and over one-third of all the grass species known from the conterminous United States occur in Texas. Although the dust jacket states that the book is intended for the botanist and the rancher with little specialized training, Dr. Gould has presented us with a complete and taxonomically rigorous treatment that is probably too advanced to appeal to the casually interested rancher or naturalist.

Introductory material on the structure of the grass plant and spikelet terminology is well done and adequately illustrated. These discussions, along with those of the vegetation areas of Texas, are taken primarily from earlier works of the author. The generic key is innovative in its use of some new characters and in its departure from the traditional format that employs preliminary stops at the subfamily and tribe levels. It is a welcome change. However, the key is sometimes awkward because of a mixture of generic names, lettered groups, and numbered groups that must be properly traced.

The system of subfamilies and tribes used by Gould is one that is gaining general acceptance. Perhaps only the names Pooideae and Poeae might be unfamiliar to many of us who have watched the once widely accepted scheme of George Bentham undergo major revisions. Gould's elevation of *Dichanthelium* and his acceptance of *Hemarthria* and *Coelorachis* mark a further adjustment in the generic names of U. S. grasses.

Descriptions of the taxa are well done. The information is complete and the use of bold-face type for scientific names and italics for subheadings makes for easy reading. While Gould generally follows recent or standard monographic treatments, his decision to recognize only about one-third of the *Dichanthelium* entities listed for Texas by Hitchcock and Chase is a most admirable exception. The systematic or agronomic commentary that accompanies many of the descriptions is both interesting and useful. Distribution of a species within the state is given in terms of the vegetation regions; general distribution is also cited.

The illustrations, particularly those of Valloo Kapadia, add much to the appearance and utility of the book. Most of the drawings, however, are taken from previously published works of the author and from other sources. Because of stylistic differences, the variation in the drawings is sometimes mildly distracting.

Texas now has a first-rate grass flora, certainly more modern and probably better than that of any other state. Students of agrostology have an important new reference.—James Payne Smith, Jr., Department of Biology, Humboldt State University, Arcata, California 95521.

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A NEW SPECIES OF SYMPLOCOS (SYMPLOCACEAE) FROM MEXICO

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Symplocos, last treated monographically by Brand (1901), continues to yield numerous novelties of local distribution from montane regions of the neotropics. My purpose here is to describe another local endemic that came to my attention in the course of field studies in Oaxaca.

Symplocos austromexicana Almeda, sp. nov. Frutex ad 2 m altus. Folia glabra, integra, petiolata, ovata vel elliptico-ovata, ad basem acuta, ad apicem obtusa vel rotundata. Lamina (0.6–)1.0–1.7(–2.0) cm longa et 0.5–0.9 cm lata. Inflorescentia uniflora; calyx 2–3 mm longus, lobis ovatis vel suborbiculatis, ciliolatis et glandulosis; corolla violacea, cylindrico-campanulata, 6–7 mm longa, glabra, lobis oblongis, obtusis et 2.5–3.5 mm latis. Stamina 24–30, triseriata. Stylus glaber, 5–7 mm longus; stigma capitata, trilobata. Fructus glaber, drupaceus, 9–12 mm longus. Fig. 1.

Robust shrub 2 m tall, perhaps attaining arborescent dimensions. Older branches glabrate, terete, minutely striate to rugulate; upper branchlets moderately covered with spreading, basally pustulate, brown trichomes mostly less than 1 mm long; immature branchlets thinly strigillose with apical buds typically white-strigose. Petioles shallowly canaliculate, thinly strigose to glabrous, (1–)2–3(–4) mm long. Principal leaves entire, coriaceous, ovate to elliptic-ovate, (0.6–)1.0–1.7(–2.0) cm long and 0.5–0.9 cm broad, apically obtuse to rounded, basally acute, glabrous on both surfaces; median nerve impressed but evident above, primary and secondary veins prominulous, evident beneath as a slightly bullate, openly reticulate network. Flowers solitary, erect or nodding, axillary, borne along distal branchlets; pedicels terete, strigillose to sericeous, 2–4 mm long, sometimes bearing 3–5 sessile, caducous bracts; these oval or oblong but varying to triangular or subulate, apically obtuse, rounded, or acute, 1.0–1.5 mm long and 0.5–1.0 mm broad, margins ciliate, otherwise glabrous with a granular, vernicose luster. Bracts evenly spaced along the floral pedicel or congested and then closely subtending the ovary and calyx lobes. Calyx 4–5 lobed; the lobes imbricate, ovate to suborbicular, 2–3 mm long, 1–2 mm wide at the base, glabrous on both surfaces, margins erose, often ciliate and provided with brown globular glands. Corolla sympetalous, glabrous, cylindric-campanulate, 6–7 mm long, 6–8 mm in apical diameter at anthesis, 6–7 lobed, purple or lavender; lobes fused basally for about 1 mm and adnate to the filament tube for the basal half of the corolla, imbricate, biseriate, oblong, apically

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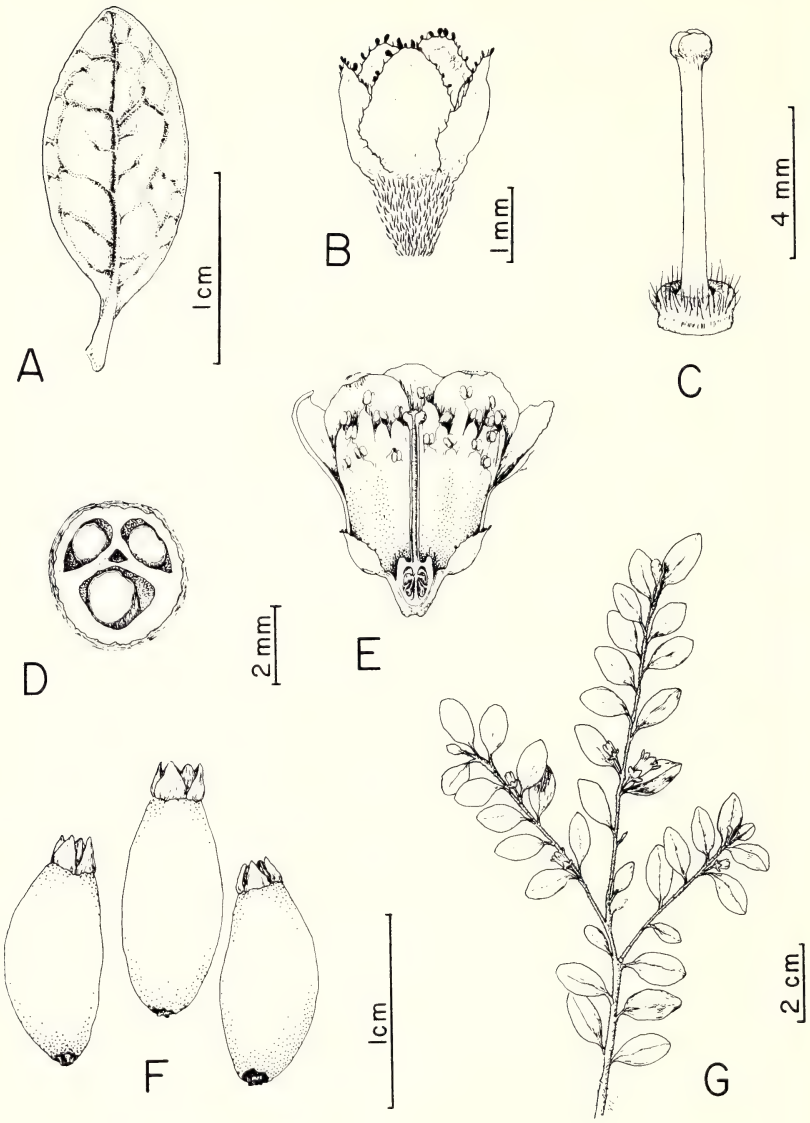

FIG. 1. *Symplocos austromexicana* Almeda. A, abaxial surface of a typical leaf; B, ovary and calyx lobes showing ciliate, glandular margins; C, style, stigma, and circular disc crowning the ovary; D, cross-section of ovary showing only one of two ovules in each locule; E, floral dissection showing half-inferior ovary, imbricate corolla lobes (one lobe removed), filament tube and triseriate staminal arrangement; F, mature fruits with persistent calyx lobes; G, habit. (A-C,E,G from *Almeda and Luteyn 1659;* D,F from *MacDougall 15.*)

rounded, 2.5–3.5 mm wide, margins entire to erose-ciliolate. Stamens 24–30, triseriate; filaments white to lavender, connate to near their apices and forming a tube slightly shorter than the corolla but equalling or exceeding the style; free portions of the staminal filaments ligulate, glabrous, 0.5–2.0 mm long. Anthers globose, white, 0.5 mm long. Ovary half-inferior, finely strigillose, about 1 mm long at anthesis and crowned by a puberulent circular (nectariferous ?) disc surrounding the style base. Style linear, glabrous, 5–7 mm long; stigma capitate, shallowly to deeply trilobed. Fruit drupaceous, glabrous, carnose at maturity, broadly ovoid to oblong-ellipsoid, 9–12 mm long, 4–8 mm broad, trilocular with two ovules usually present in each locule.

Type: Mexico, Oaxaca, about 27 miles N of Ixtlan de Juarez off of Hwy. 175 in wet pine-hardwood forests, ca 2575 m, 20 Dec 1972, *Almeda and Luteyn 1659*. Holotype: DUKE.

Distribution: Presently known only from north-central Oaxaca where it apparently occurs as an infrequent element of pine-hardwood forests between 2575 and 2880 m.

Specimens examined: Oaxaca, near gap in Sierra Juarez above Valle Nacional at ca 2727 m, 26 Dec 1970, *Sharp #MEX-717* (NY); Comaltepec, near Paso Cerro Pelon at 2880 m, 2 Sep 1966, *MacDougall 15* (US); Cerro de Humo Chico, Comaltepec, Ixtlan, 8 Feb 1966, *MacDougall 19* (US).

The small glabrous leaves, basally pustulate cauline trichomes, solitary flowers, glabrous style, and trilocular ovary serve to distinguish this species from all congeners in Mexico. Although two ovules are generally produced in each locule of the ovary, only one seed appears to develop in any one fruit. Consequently, the drupaceous fruits often become conspicuously ventricose at maturity.

There is a striking vegetative resemblance between *S. austromexicana* and *S. ovalis* Wright ex Griseb., a species endemic to western Cuba. The leaves of both species are glabrous and coriaceous with entire, revolute margins and prominulous, openly reticulate abaxial venation. Despite these vegetative similarities, there appears to be no close relationship between these taxa since *S. ovalis* differs consistently in its modally obovate leaves, racemose or paniculate inflorescences, pentamerous flowers with free petals, 40–50 stamens in several unequal series, free filaments, and lack of a conspicuous disc surrounding the apex of the ovary.

The trilocular ovary and the well defined filament tube adnate to the sympetalous corolla allow provisional placement of *S. austromexicana* in subg. *Symplocos* (subg. *Eusymplocos* in Brand), subsect. *Pseudoalstonia* of Brand's monograph. Within this subgenus, the closest affinities of *S. austromexicana* appear to be with *S. quindiuensis* Brand, a Colombian species, and *S. speciosa* Hemsley, also known only from the mountains of Oaxaca. These three taxa share such characters as a sympetalous corolla, triseriate staminal arrangement, and linear style. *Symplocos quindiuen-*

sis and *S. speciosa* differ most notably from *S. austromexicana* in their larger lanceolate leaves (6–12 cm long) having long apiculate to caudate-acuminate apices and short-pedicellate flowers disposed in congested racemes or subsessile fascicles.

Virtually nothing is known about the breeding system or pollination biology of *Symplocos* but the flowers of most species possess all the earmarks of entomophily and in some cases ornithophily. The flowers of *S. austromexicana* are homogamous and pollen release is accompanied by a slight inward bending of the free portions of the filaments to form a cluster of anthers crowning or closely adhering to the receptive stigma. Copious pollen deposition on stigmas was even noted on several unexpanded flowers examined in the field. Despite these observations, lack of information on compatibility relationships precludes a definitive statement on the breeding system at this time.

Acknowledgments

I thank Gabrielle Raumberger for meticulous care in preparing the line drawings and the curators and staffs of the following herbaria for loans of specimens: DUKE, F, K, LL, MICH, NY, TEX, US.

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THORNEA (HYPERICACEAE), A NEW GENUS FROM MEXICO AND GUATEMALA

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Several collections of two species originally placed in *Hypericum* were made by Breedlove during recent years in connection with his study of the flora of Chiapas. They are distinct enough to warrant generic status. We call the new genus *Thornea*.

Comparison of floral morphology of *Thornea* and *Triadenum* Rafin. (see Wood and Adams, 1976) indicates that they are related. We believe that *Thornea* is allied with *Triadenum* rather than with the large, variable, and widely distributed genus *Hypericum*.

Floral characters of *Thornea* and *Triadenum* show their strongest resemblance in arrangement of the stamens. Both genera have nine fertile stamens grouped in three fascicles of three each, alternating with three sterile staminodial fascicles (or fasciclodes, Robson, 1972). Petals of *Thornea* and *Triadenum* are light or dark pink and greenish-white with parallel striations. In both genera, the ovaries are 3-carpellate and develop into three nearly separate dehiscent capsules.

Thornea and *Triadenum* differ in habit: *Thornea* is a shrub whereas *Triadenum* is herbaceus. Other differences are seen in capsule and seed characters. Mature capsules of *Triadenum* have styles less than one-quarter the total length of the capsule, while in *Thornea* the styles are about one-half as long as the capsules. Seeds in both genera are oblong and small (about 1 mm long). They are more numerous in *Triadenum,* with more than ten per carpel, while in *Thornea* there are fewer than ten in each carpel. In *Thornea,* they are lightly reticulate with a minute appendage on one end or narrowly winged along one margin, while in *Triadenum* the reticulations are well developed and the seeds lack a wing or an appendage.

Thornea is a Neo-Tropical woody relative of the herbaceous temperate, widely disjunct genus *Triadenum* (Wood and Adams, 1976). Both genera, according to Robson (pers. comm.), show floral and seed similarities with the paleo-Tropical woody genus *Cratoxylum,* which suggest that the newly proposed genus should be placed with *Triadenum* in the *Cratoxyleae.*

Thornea Breedlove & McClintock, gen. nov. Frutex sempervirens, foliis oppositis punctatis; inflorescentia cymosa triflora; sepala 5; petala 5, rosea et alba; androecium 9 fertilibus staminibus, in 3 fasciculis 3 fertilibus staminibus alternantibus 3 sterilibus fasciculis ordinatum; capsula paucis seminibus; semina margine alata angusto, testa modice reticulata.

Evergreen shrubs, glabrous; leaves opposite, entire, punctate, especially on lower surface, chartaceous or subcoriaceous; inflorescences terminating lateral branches, cymose, 3-flowered; sepals 5, striate; petals 5, pink and white, oblong, striate, imbricate in bud, later more or less reflexed; androecium of 9 fertile stamens in 3 fascicles of 3 stamens each alternating with 3 sterile staminodial fascicles, anthers 2-celled, filaments gradually dilated toward base; gynoecium 3-carpellate, each carpel with 1 style; capsules dehiscing at maturity nearly to the base of the carpels, styles persistent, about ⅓ the length of each carpel; seeds few in each carpel, oblong, small, lightly reticulate to almost smooth, with a narrow wing along one margin or a terminal appendage.

Type species: *Thornea matudae* (Lundell) Breedlove & McClintock.

Genus named for Robert F. Thorne, eminent phylogenist and student of the Mexican flora, of Rancho Santa Ana Botanic Garden, Claremont, California, who with Dennis Breedlove made the first Mexican collection of *Thornea calcicola* in Chiapas in 1971.

The two species of *Thornea,* though restricted in their distribution to southern Chiapas and adjacent northern Guatemala, occur in different habitats.

They are distinguished from each other on the basis of the following key.

Densely branched, internodes short to 0.5 cm long; leaves subcoriaceous, 0.5–1.5 cm long, base of blade attenuate, scarcely auriculate; flowers dark rose-pink, petals 5 mm long; capsules to 5 mm long. *T. calcicola*

Openly branched, internodes longer, to 1.5 cm long; leaves chartaceous, 1.0–4.5 cm long, base of blades biauriculate; flowers pink and white, petals 7 mm long; capsules to 7 mm long. . . . . *T. matudae*

Thornea matudae (Lundell) Breedlove & McClintock, comb. nov. *Hypericum matudae* Lundell (as *H. matudai*), Bull. Torrey Bot. Club 69:394–395. 1942. TYPE: Mexico, Chiapas, Mt. Paxtal (Cerro Paxtla on Mexican maps), 27 Dec 1936, *Matuda 499*. Holotype: MICH.

Shrub about 2 m tall; leaf blades oval, 1.2–4.5 cm long; 0.6–2.0 cm wide, chartaceous, apex rounded, base cuneate, decurrent, biauriculate, auricles incurved, petioles 2–7 mm long, pedicels slender, 4–7 mm long; sepals ovate, 2–3 mm long, margins sparingly fimbriate; petals 6–7 mm long, pink and white; stamens 4–6 mm long; capsules 6–7 mm long; seeds 1 mm long, sparsely reticulate to almost smooth, narrowly winged along one side. Fig. 1.

SPECIMENS EXAMINED (in addition to type): Mexico, Chiapas, Municipio of Siltepec, ridge above Siltepec on road to Huixtla, 2000–2400 m, *Breedlove 31990 and A. R. Smith.*

The collection from near Siltepec was a single shrub in the dense shaded understory of a well developed Montane Rain Forest on a steep north-facing slope. The substrate was formed of sedimentary shales and sandstone of late Paleozoic and early Mesozoic origin. The forest was 25–40 m tall with a single canopy and a dense, diverse understory. Canopy trees included *Cleyera theoides, Symplocos, Clethra, Matudea, Saurauia, Pinus chiapensis, Quercus* ssp., *Cyathea, Nectandra, Ocotea, Buddleia, Topobaea,* and *Perrottetia.*

The type collection (*Matuda 499*) was made some 25 km southwest of the above locality in the same geologic formation and the same section of the Sierra Madre called the Sierra de Soconusco. The type was a unicate, and although Matuda subsequently made some 10,000 collections in this general region, he apparently never encountered *Thornea matudae* again.

Thornea calcicola (Standley & Steyermark) Breedlove & McClintock, comb. nov. *Hypericum calcicola* Standley & Steyermark, Publ. Field Mus. Nat. Hist., Bot. Ser. 23:64–65. 1944. TYPE: Guatemala, Department of Huehuetenango, Sierra de los Cuchumatanes, 6 Aug 1942, *Steyermark 50160*. Holotype: F.

Shrub to 3 m tall, densely branched, numerous short lateral branches, internodes short, 2–5 mm long; leaves oblong to oval, obtuse at apex, acute to abruptly attenuate at base, reticulately veined beneath, subcoriaceous, 5–15 mm long, 2–6 mm wide, petioles 1–2 mm long; pedicels slender, to 5 mm long; sepals ovate, 2 mm long, pink, margins fimbriate; petals oblong, 5 mm long, rose red; stamens to 4 mm long; capsules 5 mm

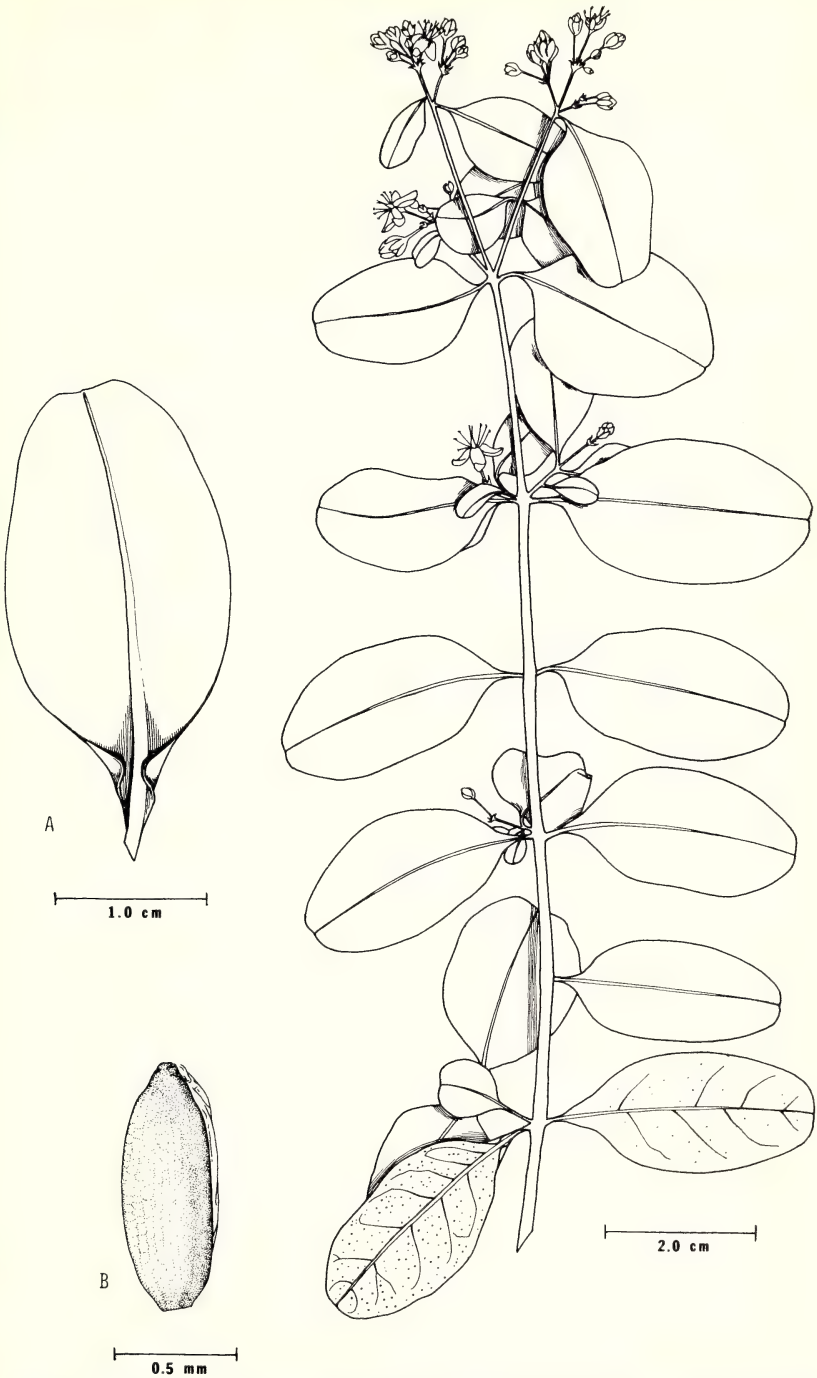

FIG. 1. *Thornea matudae.* A, leaf blade, biauriculate at base; B, seed. (*Breedlove 31990 and A. R. Smith,* DS).

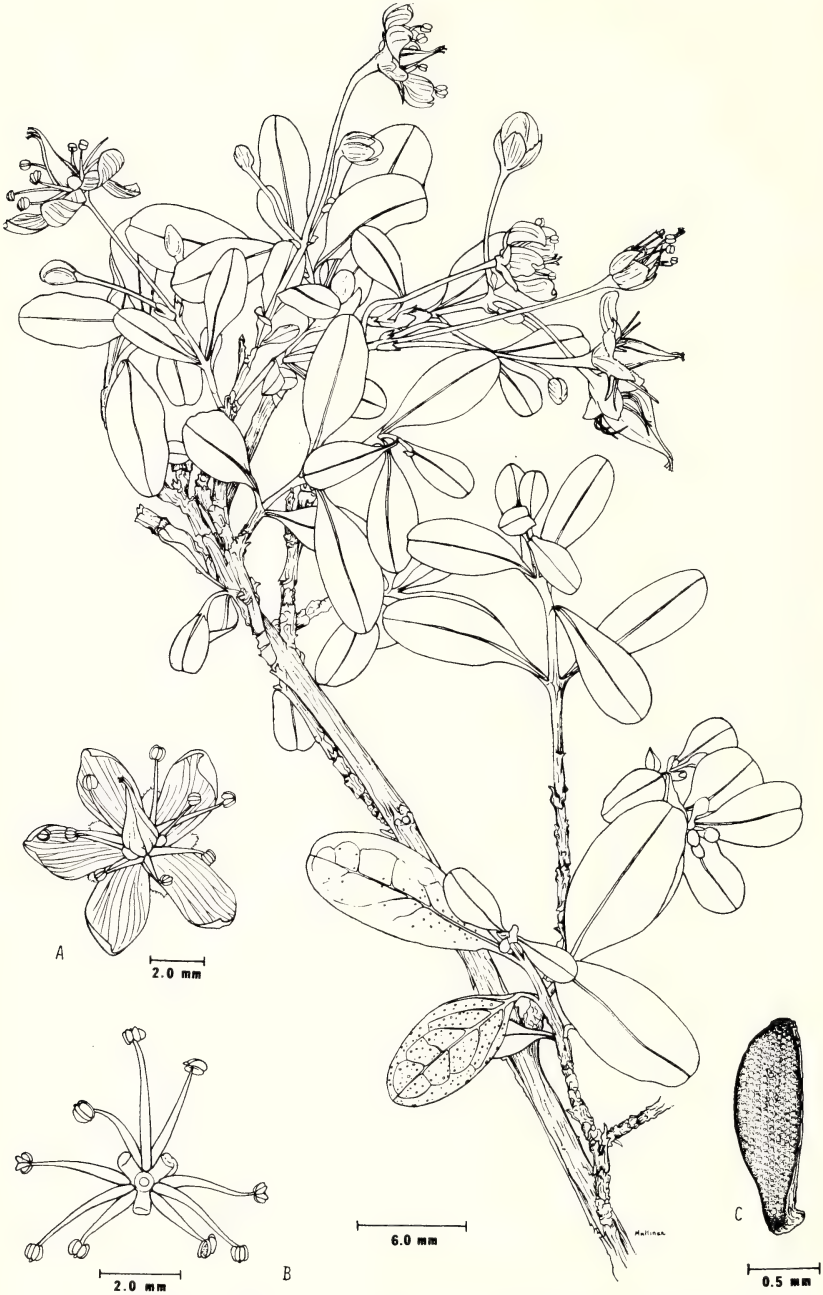

FIG. 2. *Thornea calcicola.* A, flower; B, androecium; C, seed. (*Breedlove 27561,* DS).

long; seeds oblong, 1 mm long, lightly reticulate, with small terminal appendage at one end. Fig. 2.

SPECIMENS EXAMINED (in addition to type): Guatemala, road to San Juan Ixcoy, Sierra de los Cuchumatanes, 3700 m, *Molina R., Burger, and Wallenta 16469,* F. Mexico, Chiapas, Municipio of La Trinitaria, Monte Bello National Park, 1300 m, 42 km northeast of La Trinitaria, *Breedlove 27561,* DS; same locality, *Breedlove 21104 and R. F. Thorne,* DS, *Breedlove 36937,* DS; slopes with Montane Rain Forest, *Liquidambar, Magnolia, Vochysia,* east of Laguna Tzikaw, *Breedlove 32254,* DS; Laguna Pojoj near Laguna Tsiskaw, *Breedlove 37070,* DS.

In Chiapas, *Thornea calcicola* is a locally abundant shrub often becoming sub-dominant. It occurs in a shrubby evergreen formation reminiscent of an "elfin forest", a modification of the Montane Rain Forest, which occurs on Miocene limestone slopes on the shores of many of the lakes in the Lagos de Monte Bello National Park in south-central Chiapas on the Guatemala border. Associated trees and shrubs include *Rondeletia stenosiphon, Podocarpus matudae, Cavendishia laurifolia, Saurauia scabrida, Lyonia squamulosa, Litsea, Hoffmannia, Daphnopsis, Tibouchina breedlovei, Monnina xalapense, Hauya heydeana, Zanthoxylon, Parathesis chiapensis, Polygala floribunda,* and *Miconia laurifolia.*

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We are grateful for the loan of specimens from F. Special thanks go to Dr. Norman Robson (BM) for his advice and comments regarding the relationship of *Thornea* to other members of the Hypericaceae. The drawings were made by Carolyn Mullinex.

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A NEW SPECIES OF CHRYSACTINIA (COMPOSITAE: TAGETEAE) FROM SINALOA, MEXICO

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Recent collections from the mountains of northern Sinaloa include a previously undescribed species of *Chrysactinia* A. Gray. As last revised (Blake, 1916), *Chrysactinia* comprised four species of eastern and central Mexico and the southwestern United States. The new species, *C. lehtoae,* is the first *Chrysactinia* known from western Mexico.

Chrysactinia lehtoae differs markedly from previously described taxa. *Chrysactinia pinnata* S. Wats. and *C. truncata* S. Wats. are similar to *C. lehtoae* in having pinnately divided leaves, but leaves of these two species differ from those of *C. lehtoae* in shape of lobes and in distribution and number of oil glands (fig. 1). The two remaining species, *C. mexicana* A. Gray and *C. acerosa* Blake, have short, linear or acicular, entire leaves. *Chrysactinia lehtoae* resembles *C. truncata* in having 13-rayed heads with yellow ligules, whereas *C. pinnata* has 8-rayed heads, and the ligules are bicolored, white above and orange beneath. J. L. Strother (pers. comm.) has indicated that *C. lehtoae* is so different from *C. pinnata* and *C. truncata* that it probably merits separation from these species at the sectional level.

Chrysactinia lehtoae is named in honor of Mrs. Elinor Lehto, Curator of the Herbarium at Arizona State University since 1966. Mrs. Lehto is a student and avid collector of the flora of the southwestern United States and northern Mexico.

Chrysactinia lehtoae Keil, sp. nov. (fig. 1). Suffrutex e basi ramosus, caulibus foliosis, usque ad circa 3 dm longis, viridibus vel spadiceis, sexcostatis, glabris. Folia decussata, semel pinnatipartita fere ad nervum medium; bases petiolorum parum expansae, trichomatibus multicellularibus 0.2–0.4 mm longus ciliolatae, lineis connatis ciliolatus connexae; petioli exiles, 4–8 mm longi, adaxiale trichomatibus circa 0.2 mm longis puberuli, abaxiale glandibus pellucidis linearibus 1–4 mm longis punctati; rhaches exiles 10–13 mm longae, angustissime alatae, adaxiale sulcatae et trichomatibus circa 0.2 mm longis puberulae, abaxiale glandibus pellucidis linearibus vel ellipticis 0.5–1.0 mm longis punctatae; foliola 5–9, linearia, 10–22 mm longa, 1–2 mm lata, integra vel minute crenulata, acuminata, cuneata, uninervata, adaxiale nervo medio trichomatibus circa 0.2 mm longis puberulenta, in marginibus ambabus et in pagina abaxiale prope basin glandibis pellucidis ellipticis 0.3–0.7 mm longis punctata. Capitula radiata, solitaria terminaliaque in pedunculis 17–20 mm longis, bracteolas lineares 2–3 mm longas ferentibus. Involucrum campanulatum; phyllaria 13, uniserialia, subaequalia, oblonga 4–5 mm longa, circa 1 mm lata, versus apicem obtusam angustata, basaliter truncata, dorsale convexa, carinata induratagque, margine membranacea, versus apicem trichomatibus multicellularibus circa 0.1 mm longis ciliolata, aliter glabra, glande pellucida elongata mediali solitaria subterminali 2–3 mm longa et in dimidio inferiore uno vel duobus paribus glandium submarginalium linearium seu ellipticorum 0.3–1.0 mm longorum punctata. Flosculi ligulati 13; corollae luteae, tubis 3 mm longis, trichomatibus multicellularibus circa 0.1 mm longis sparse puberulentis, ligulis oblongis 7 mm longis, 2–3 mm latis, ad apicem minute tridentatis, utrinque glabris. Flosculi tubuliflori numerosi; corollae flavae vel flavovirentes, circa 6 mm longae, in tuba et fauce vix differentiatae, trichomatibus multicellularibus circa 0.1 mm longis sparse puberulentae, lobis 5 triangularibus aequalibus ascendentibus 0.5 mm

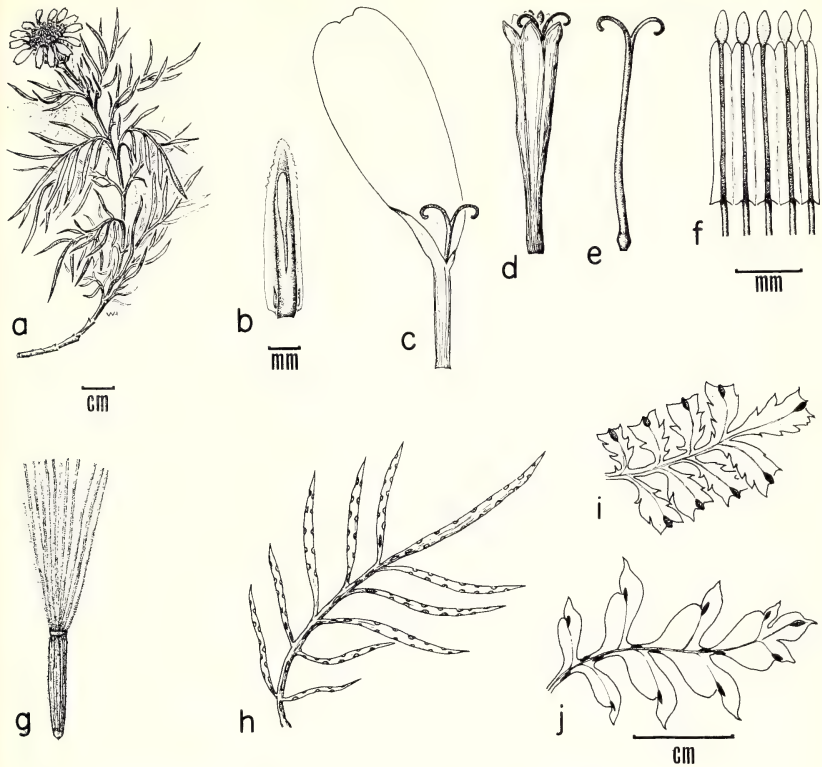

FIG. 1. a—h, *Chrysactinia lehtoae* (*Lehto et al. L19551,* ASU). a, habit; b, phyllary; c, corolla of ray floret; d, corolla of disc floret; e, style of disc floret; f, anthers; g, achene; h, leaf. i, leaf of *C. truncata* (*Stanford et al. 833,* ARIZ). j, leaf of *C. pinnata* (*Stanford et al. 310,* ARIZ). b—e, g all same scale; h—j all same scale.

longis; antherae thecis circa 2.5 mm longis, basaliter minute sagittatae, appendice terminali deltoidea circa 0.5 mm longa; pollinis grana echinata, circa 23μm diametro; rami styli recurvati circa 1 mm longi, apicibus truncatis. Achenia flosculorum ligulatorum tubuliflorumque similaria, nigra, subcylindracea, vix compressa, 3 mm longa, 0.7 mm diametro, multinervata, trichomatibus usque ad 0.1 mm longis minute puberulenta; carpopodium eburneum glabrum triangulare obliquum 0.3 mm longum et latum; setae capillares pappi 20–30 albidae, antrorse barbellulatae, usque ad 5.5 mm longae. Chromosomatum numerus ignotus.

TYPE: Sinaloa, 18 mi NE of Choix, very close to Chihuahuan border, ca. 26° 50′ N, 108° 11′ W, 1300 m, 25–26 Nov 1975, *T. H. Nash, J. J. Landye, and E. Lehto L19551.* Holotype: ASU. The type was collected on a limestone outcrop on a steep mountain slope in an open oak-pine forest.

ACKNOWLEDGMENTS

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A NEW SPECIES OF CLAUDOPUS FROM NORTHERN CALIFORNIA

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Eight species of *Claudopus sensu* Largent and Benedict (1971) have been reported from the Pacific Coast of the United States (Largent and Thiers, 1972). Three of these, *Claudopus nidulans* (Pers. ex Fr.) Karsten, *C. commixtus* Bres., and *C. variabilis* (Pers.) Gillet, have been transferred to *Phyllotopsis, Pleurotellus,* and *Crepidotus,* respectively (Singer, 1975). Three, *C. affinis* Kauff., *C. corticinctus* Kauff., and *C. subargillaceus* Kauff., have smooth basidiospores and have been excluded from the rhodophylloid fungi (Largent, 1971). The remaining two, *C. byssisedus* (Pers. ex Fr.) Gillet and *C. avellaneus* Murr., have pinkish, angular basidiospores and are good species of *Claudopus* (Hesler, 1963; Largent, 1974). The former species has been reported from Washington, Oregon, and California (Kauffman, 1929; Largent, 1974); the latter species has been reported from Oregon (Murrill, 1917).

This report contains a description of a previously undescribed species of *Claudopus,* which represents the second verified species of this genus from California. Abbreviations used in the description and methods of measuring the spores will be found in my study of *Claudopus byssisedus* (Largent, 1974). Color terms used in the description are from Kornerup and Wanscher (1961). The terms *pileipellis, suprapellis, subpellis,* and *stipitipellis* are used in the same sense as Bas (1969).

Claudopus graveolens Largent, sp. nov. Pileus plano-convexus, bicolor, ad centrum pallide griseibrunneus, alibi atrobrunneigriseus, glaber, haud hygrophanus, margine decurvato, integro, non striato. Odore forti, mephitico. Stipes minutus, excentricus vel lateralis, griseibrunneus, strato denso fibrillarum albidis obtectus.

Cheilocystidia sparsa vel abundantia, hyalina, versiformia. Pleurocystidia desunt. Pileipellis bistrata. Trama pilei heterogenea, ex hyphis lati-

ciferis sparsis, hyphis gracilibus 2–4 μm crassis incrustatis, et hyphis perlatis, inflatis, non incrustatis 12–15 μm crassis constans. Stipitipellis bistrata. Caulocystidia desunt. Pigmentum in vacuolis hypharum praeter hypas incrustatas tramae pilei. Fibulae basi basidiorum adsunt, in hyphis pileipellis rarae, in hypis stipitipellis non visae.

TYPE: California, Trinity Co., at the end of Canyon Creek Road, Shasta-Trinity National Forest, on soil at the margins of a depression and beneath a layer of straw, 10 Nov 1973, *Largent 6579*. Holotype: HSC.

Pileus 7 mm broad, 2 mm high, plano-convex to plane and ovoid in outline; bicolorous with the apical area light grayish brown (6–7,C–D,4) and the remaining portion dark brownish gray (6–7,F,2); surface glabrous, dry, non-hygrophanous, and margin decurved, entire and not translucent-striate; context up to 0.5 mm thick and concolorous with the pileal surface; odor very strong and skunk-like, penetrating and permeating the collecting bag and persistent. Lamellae subdecurrent, subdistant, narrow, 1.5 mm wide, 2.5 mm long, and gray. Stipe minute, 1.5 mm wide, 4.0 mm long, equal, eccentrically to laterally attached, gray-brown and covered by a dense layer of whitish fibrils that are entangled with the hyphae of the basal tomentum.

Spores 8.0–10.0 by 6.0–7.5 μm, average length 8.9 μm, average width 6.8 μm, elongate-angular, L-D 1.5–3.5 μm (average 2.1 μm), 5–6-sided. Basidia 4-spored, clavate, 25–30 by 8–9 μm). Cheilocystidia scattered to abundant, colorless, versiform in shape, often either capitate or strangulated, (25–45 by 5–10 μm, capitate apex 5–10 μm, average length 32.9 μm, average width 6.9 μm); pleurocystidia absent. Pileipellis two-layered; suprapellis a cutis, hyphae repent, at times with an uplifted cylindroclavate terminal cell; subjellis tightly entangled. Pileal trama heterogenous, with scattered lactifers and two types of hyphae—very slender hyphae 2–4 μm in diameter with external incrustations, soluble in 3% KOH, interspersed with very broad, inflated, non-incrusted hyphae 12–15 μm in diameter. Stipitipellis two-layered; suprapellis a layer of entangled, narrowly cylindric hyphae 1–3 μm in diameter, at times with capitate to swollen apices, 5–8 μm in diameter; subpellis a cutis. Caulocystidia absent. Pigmentation vacuolar except for the externally incrusted slender hyphae that ramify throughout the pileal trama. Clamp connections present at the base of the basidia; rare on the hyphae of the pileipellis; absent at the base of the basidia and not observed on the hyphae of the stipitipellis.

Unique features of *Claudopus graveolens* are its penetrating mephitic odor, minute pleurotoid stature, heterogenous pileal trama, external incrustation on the narrow hyphae of the pileal trama, and whitish fibrils covering the stipe.

The only other *Claudopus* from North America with an odor similar to *C. graveolens* is *Claudopus mephiticus* Murr., which is distinctive due to its greenish- or yellowish-white pileus. *Claudopus byssisedus* is dis-

tinguished by its greyish orange to brownish orange pileus, its dense, whitish universal veil, and its farinaceous taste and odor; *C. avellaneus* is distinguished by its pale-avellaneous, finely tomentose pileus and its mild odor and taste.

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GALIUM MEXICANUM (RUBIACEAE) OF CENTRAL AMERICA AND WESTERN NORTH AMERICA

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Galium mexicanum Kunth, in the present expanded sense, occurs in mountainous areas from Panama northward and westward to the state of Washington near the Canadian border (fig. 1) and on Socorro Island. It has not been collected in northeastern Mexico nor in Baja California.

The species was described in 1818 by Kunth (type near Guanajuato) with "*foliis octonis*". In 1849, Gray published *Galium asperrimum* (type from New Mexico) with "*foliis omnibus senis*" and with some considerable floral differences, which he did not mention. He followed this in 1880 with *G. asperrimum* var. *asperulum* from California, based principally on leaf characters. In 1898, Greenman named two varieties of *G. mexicanum,* namely var. *glabratum* from Oaxaca, based on lack of hairs, and var. *platyphyllum,* based on leaf shape and indumentum, with citation of specimens from Chiapas, Oaxaca, and Jalisco. There are thus currently five names, of which I propose to recognize the first three, while changing the status of *G. asperrimum* Gray and its var. *asperulum* Gray to subspecies of *G. mexicanum*. A new subspecies has been added,

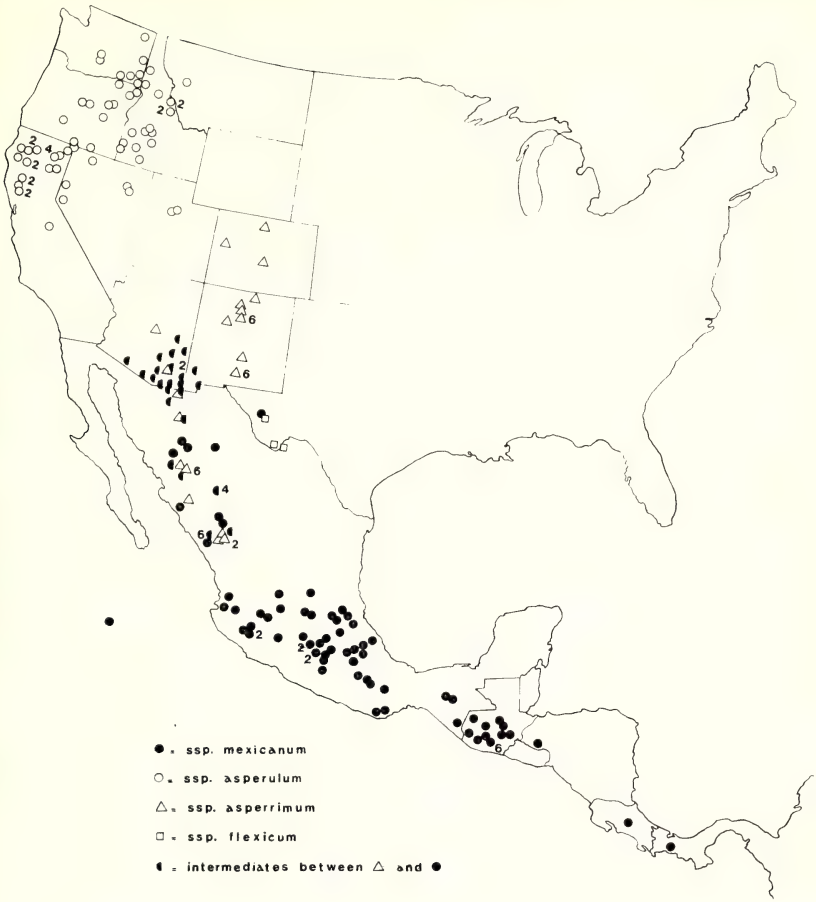

FIG. 1. Distribution of the subspecies of *Galium mexicanum*. Numbers (2, 4, and 6) refer to diploid, tetraploid, and hexaploid chromosome counts.

and the Greenman varietal names are treated as synonyms of ssp. *mexicanum*.

Galium mexicanum is a perennial herb with 5–12 "leaves" at each node (most commonly 6), few to many aculeolate hairs on stems and leaves, perfect flowers having generally, but not always, campanulate corollas, and fruits with well developed (fig. 2 A′, G′) or obscure (fig. 2 B′) uncinate hairs. Where the hairs are obscure, the fruits appear to be tuberculate, although hairs are visible under a dissecting microscope. Very rare individuals (as in perhaps all *Galium* species) have glabrous ovaries and fruits (fig. 2 E).

Although the number of leaves to a node varies in all of the subspecies, the character is somewhat clinal, the tendency being toward a lower number in the northern subspecies and a higher in the southern sub-

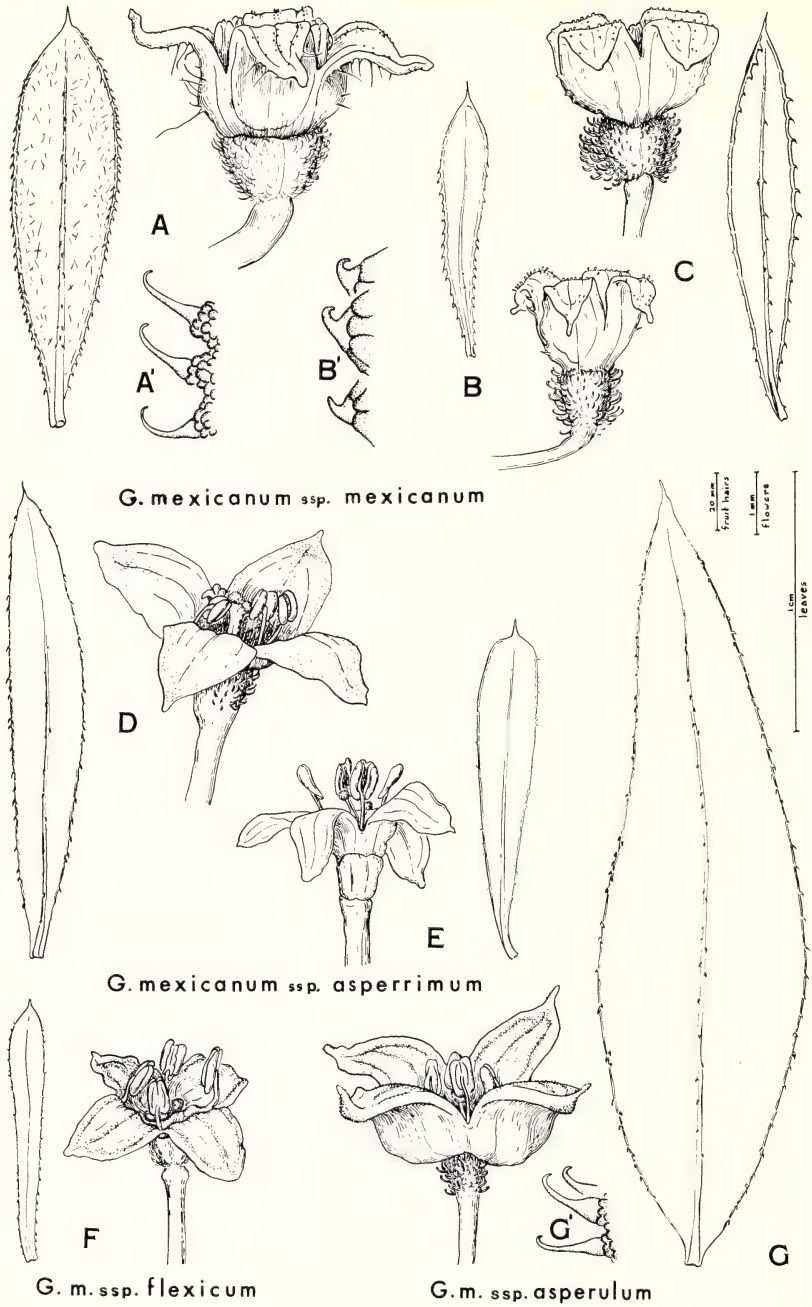

FIG. 2. Representative leaves, flowers, and fruit hairs of *Galium mexicanum*. A-C, ssp. *mexicanum*; D-E, ssp. *asperrimum*; F, ssp. *flexicum*; G, ssp. *asperulum*.

species. The commonest and apparently the "basic" number for *G. mexicanum* throughout is six leaves per node (i.e., two leaves and four stipules), with five to ten not uncommon. Supernumerary leaves occur most often where strong branches arise. The *"foliis octonis"* of Kunth and the *"foliis omnibus senis"* of Gray are both over-simplifications, although Gray was the more nearly correct.

Leaf shape is also somewhat clinal. The leaves of ssp. *asperulum* of the north are thin and generally elliptical or lanceolate, being broadest at or below the middle, in contrast with the often strongly oblanceolate, often leathery, leaves of ssp. *mexicanum* in the south, and in moderate contrast with those of ssp. *asperrimum* of the middle latitudes. Within ssp. *mexicanum* the leaves, although nearly always broadest above the middle, vary greatly in shape, from nearly linear to broadly oblanceolate, without relation to floral characters or geographic location. Hence, Greenman's var. *platyphyllum,* based on a miscellaneous collection of broad-leaved specimens from various localities, is untenable. Leaves in the northern plants are demonstrably larger on the average, and the internodes correspondingly smaller, than in the southern plants (Table 1).

Kunth gave an adequate description of the flowers of *G. mexicanum.* Gray, however, said little about the flowers of *G. asperrimum* and essentially nothing about those of var. *asperulum*; yet flower characters offer the most satisfactory basis for separating these taxa from ssp. *mexicanum* (see key). These flower differences are, in fact, sufficiently impressive that, were it not for massive intergrading in Durango, Chihuahua, Sonora, and Arizona, it would seem reasonable to follow Gray's plan, with a separate species (*G. asperrimum*) typified in New Mexico and a variety (*asperulum*) typified in California.

Galium mexicanum does not divide neatly and easily into subspecies, although many local genetic races exist, as indicated, for example, by rotate corollas near Espinazo del Diablo in Durango, "tuberculate" fruits in the Chiricahua and Huachuca mountains, Arizona, and red or pink corollas in Guatemala and Chiapas.

Separation of ssp. *asperulum,* geographically removed in the far northwest corner of the range, seems clearly desirable, although the morphological characters that separate it are subtle. The establishment of a new subspecies in northern Coahuila and western Texas also seems justified, despite the relatively small area that it occupies, because its range is marginal to the whole and the morphological characteristics are striking and consistent within that range. Subspecies *asperrimum,* on the other hand, is more open to question. In Colorado and New Mexico, except in the southwest corner (Grant Co.), this subspecies is consis-

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A, Jalisco, *McVaugh 11679;* A′, Puebla, *Nicolas s.n.*; B, Oaxaca, *Iltis 1151*; B′, Arizona, Huachuca Mts., *Lemmon 3013*; C, Distrito Federal, *Pringle 6518*; D, New Mexico, *Wooton s.n.*; E, Chihuahua, *Dempster 4390*; F, Texas *Palmer 35812*; G, California, *Dempster 4444.*

TABLE 1. COMPARISON OF LEAF LENGTH AND INTERNODE INDEX OF SUBSPECIES OF GALIUM MEXICANUM. Number refers to the number of collections measured. Leaf length is the overall average measurement of the longest available leaf in each collection. The internode index is an overall average based on measurement of the longest three consecutive internodes on the leafy portion of the plant, divided by the longest contiguous leaf.

	Number	Leaf length	Internode index
ssp. *asperulum*	113	2.7 cm	6.0
ssp. *asperrimum*	50	1.7 cm	7.1
intermediates	96	1.7 cm	9.0
ssp. *mexicanum*	163	1.5 cm	9.9

tently distinct from ssp. *mexicanum*, on the basis of floral characters. It also appears in various places in Arizona and the Sierra Madre Occidental, surrounded, however, by intermediate forms. Throughout the large area including Durango, Chihuahua, Sonora, Arizona, and western Texas, corollas vary from deeply cut and spreading to more or less urceolate, with more or less sharply reflexed lobes, and the stamens are more or less conspicuous. Within this same area, however, some character expressions that are found farther south do not occur, namely pilose or colored corollas, pilose stems and lower leaf surfaces, and leathery leaves.

Although there seems to be no perfect resolution of the taxonomic problem posed by such a mass of intermediate forms, it does seem clear that the plants of New Mexico and Colorado, and of some localities in the Sierra Madre Occidental, should neither be included with those of the northwest (ssp. *asperulum*), which they somewhat resemble, nor with those of southern Mexico. If, however, a ssp. *asperrimum* is recognized, as it seems it must be, such recognition should be qualified by stating that, although nicely distinct in Colorado and New Mexico, it intergrades with ssp. *mexicanum* from southern Arizona to southern Durango.

The question arises as to whether ssp. *asperrimum* is an incipient species or an old one in the process of merging with ssp. *mexicanum*. Although one might incline toward the latter interpretation, the chromosome situation seems to contradict it. On the distribution map (fig. 1), the figures 2, 4, and 6 represent diploid, tetraploid, and hexaploid populations ($x = 11$). It is apparent that the situation is complex and that many more chromosome counts are needed for an adequate interpretation. From available evidence, it may be suggested, however, that ssp. *asperulum*, with one tetraploid and twelve diploid counts, is an ancient taxon and ssp. *mexicanum* as represented in central Mexico, with three diploid counts, is another. Since populations of ssp. *asperrimum* in New Mexico, where it is typified, and again in the Creel area of Chihuahua, are hexaploid, it cannot be considered ancient, but rather comparatively recent, and perhaps independently derived in several places. It should be noted that in the Durango area one diploid was judged to be of ssp. *asperrimum* on a morphological basis. It should be

mentioned also that the hexaploid collection from Durango was too young to have flowers and might, therefore, be assignable to ssp. *asperrimum* rather than to ssp. *mexicanum*. It seems likely that the whole central population, at least from Durango north into Colorado, represents an evolutionary mingling, with perhaps frequent polyploidy, between the several rather different diploids currently known, besides others not yet recognized.

Key to subspecies of *Galium mexicanum*.

Leaves lanceolate to elliptical, rarely a little oblanceolate, but generally broadest at or below the middle, the largest commonly (1.3)2–4(5) cm long; fruits smooth, not noticeably tuberculate beneath the hairs; corollas white, glabrous, the lobes spreading, the anthers usually visible.....ssp. *asperulum*

Leaves narrowly elliptical or linear to broadly oblanceolate, usually broadest above the middle, the largest commonly 1–2(3) cm long; fruit hairs arising from tubercles; corollas white or colored, glabrous or pilose, the lobes spreading or more or less erect from the sinuses, the anthers visible or often hidden.

Corollas white, pink, or red, sometimes pilose, often cleft about halfway, the lobes more or less erect, then sharply reflexed, the throat usually cupped or, together with the lobes, often urceolate; stamens generally included; stems and lower surface of leaves often set with long straight hairs; leaves thin or often leathery, the marginal hairs stout, retrorse.....ssp. *mexicanum*

Corollas white, not pilose, cleft usually more than halfway, the lobes spreading, not sharply reflexed, the throat flaring to nearly rotate; stamens often exserted; stems and leaves without long straight hairs; leaves thin, the marginal hairs retrorse or antrorse.

Leaves narrowly elliptical to broadly oblanceolate, the marginal hairs retrorse; flowers many, in elaborate, usually loose, terminal bracteose inflorescences and on lower lateral branches; true pedicels not exceeding 8 mm.....ssp. *asperrimum*

Leaves linear to narrowly oblanceolate, the marginal hairs retrorse near leaf base, antrorse on the apical half of the leaf; inflorescence much reduced, the flowers few, often in 3's; true pedicels often very long (to 20 mm).....ssp. *flexicum*

GALIUM MEXICANUM Kunth in HBK, Nov. Gen. et Sp. 3:337. 1818.

TYPE: Protologue cites a collection from near Guanajuato by Humboldt and Bonpland. Dr. A. Lourteig was unable to find the Humboldt and Bonpland type at P. It is to be hoped that the specimen will some day be found, but until that occurs it seems desirable to choose a neotype. Considering the local variability of the species, it is important that such neotype be from the type locality, i.e. "prope Guanaxuato,

alt. 1070 hex.". I have seen only three specimens from the state of Guanajuato, two of them from near Guanajuato city. Of these, one is incomparably better than the other in being more complete, in having fuller data and in conforming better to the original description. I therefore designate it as the neotype: 18 miles east of Guanajuato in (sic) road to Dolores Hidalgo, 17 Aug 1957, *Solbrig and Ornduff 4540* (UC).

GALIUM MEXICANUM Kunth ssp. MEXICANUM.

Galium mexicanum var. *glabratum* Greenm., Contr. Gray Herb. n. ser. 14:458. 1898. TYPE: Oaxaca, west slope Mt. Zempoaltepec, *Nelson 583*. Holotype: US!

Galium mexicanum var. *platyphyllum* Greenm., Contr. Gray Herb, n. ser. 14:458. 1898. TYPE: Chiapas, near San Cristóbal, *Nelson 3165*. Holotype: US!

Moist slopes, meadows, cliffs, and barrancas; mostly dense or open pine-oak forest, but sometimes in chaparral, or with *Abies, Juniperus, Opuntia,* or palms. (970)1200–3500 m. Panama, Costa Rica, Honduras, Nicaragua, Guatemala, south and central Mexico, northward in the Sierra Madre Occidental to eastern Sonora and southwestern Arizona; western Texas; Socorro Island. In Durango and northward, it intergrades with ssp. *asperrimum*. $2n = 22, 44, 66$ (see Table 2).

Galium mexicanum Kunth ssp. **asperulum** (Gray) Demp., comb. et stat. nov.—*Galium asperrimum* var. *asperulum* Gray, Bot. Cal. 1:284. 1880.—*Galium asperulum* (Gray) Rydb., Fl. Rocky Mts. 809. 1917.—*Galium mexicanum* var. *asperulum* (Gray) Demp., Brittonia 10:187. 1958. TYPE: California, Mariposa Co., Mariposa Sequoia Grove, *Bolander 6350*. Holotype: GH!; isotypes: UC! US!.

Wet places near streams, springs, and seeps; (150)950–3000 m. Pacific northwest from Washington and northern California east to western Montana and Utah. $2n = 22, 44$ (see Table 2).

Galium mexicanum Kunth ssp. **asperrimum** (Gray) Demp., comb. et stat. nov.—*Galium asperrimum* Gray, Pl. Fendl. 60. 1879. TYPE: New Mexico, Santa Fe, *Fendler 289*. Holotype: GH; isotypes: MO!, UC!

Wet ground along streams, and on moist slopes and meadows, 1950–3000 m. Colorado and New Mexico; isolated localities in Arizona and in the Sierra Madre Occidental in Sonora, Chihuahua, and Durango, where it also intergrades with ssp. *mexicanum*. $2n = 22, 66$ (see Table 2).

Galium mexicanum Kunth ssp. **flexicum,** ssp. nov. Planta *Galium concinnum* simulans, foliis senis tenuibus anguste oblanceolatis, floribus paucis pedicellis longis capillaribus insidens, sed corolla campanulata

TABLE 2. CHROMOSOME NUMBERS IN GALIUM MEXICANUM. Collection numbers are mine unless otherwise indicated. Vouchers are in JEPS or UC. See also Figure 1.

Galium mexicanum ssp. *asperulum.*

$2n = 22$. California, Lake Co., Rice Creek Road at Deer Creek, *4435,* Twin Springs S of Sheetiron Mtn., *4437,* Rice Creek Rd. N of Sheetiron Mtn., *4438*; Glenn Co., Big Cottonwood Flat, *Eckenwalder 203,* Cottonwood Glade, *4439*; Trinity Co., along Mad River S of Ruth, *4441*; Shasta Co., Quartz Spring on road to French Gulch, *4444*; Siskiyou Co., N Fork Coffee Creek, *4443,* Big Springs of McCloud River, *4446*. Idaho, Lemhi Co., Pierce Creek, *4465,* Panther Creek Road, *4467*. Montana, Ravalli Co., N of Sula, *4463*.

$2n =$ ca 44. California, Plumas Co., Swain Mtn. road 1.9 mi from Hwy 36, *4447*.

Galium mexicanum ssp. *asperrimum.*

$2n = 22$. Durango, W of Durango city, *4395*.

$2n = 66$. New Mexico, Otero Co., Sacramento Mts., *4385*.

$2n =$ ca. 66. New Mexico, Santa Fe Co., Sangre de Cristo Mts., *4382*. Chihuahua, Creel, *4390*.

Galium mexicanum ssp. *mexicanum.*

$2n = 22$. Arizona, Graham Co., Pinaleño Mts., *4407*. Jalisco, Hwy 10 S of junction with road to Tuxpan, *Weller 667*. Michoacan, N of San Felipe los Alzati, *Weller 739*. Mexico State, 8 mi S of Temescaltepec, *Weller 600*.

$2n = 44$. Chihuahua, hills W of Santa Barbara, *4399*.

$2n = 66$. Durango, Route 40 near Sinaloa state line, *Cruden 1170* (no flowers).

$2n =$ ca 66. Guatemala, Sacatepequez, Volcán de Agua, *Cruden 1558*.

fauce non profunda lobis extendentibus, fructibus ovariisque pilis uncinatis obtectis.

TYPE: Texas, Brewster Co., Chisos Mts., 18 Aug 1931, *C. H. Mueller 8281*. Holotype: TEX!; isotypes: GH!, MICH!, NY! The name refers to the Big Bend of the Rio Grande.

Stems slender, flexible, minutely scabrous; leaves 6 at a node, linear to mostly narrowly oblanceolate, 1–2 cm long, the margins scabrous, the lower hairs retrorse, the upper mostly antrorse; inflorescence much reduced, the flowers few (often in 3's); pedicels and branchlets of the inflorescence capillary, the true pedicels often exceptionally long (to 20 mm in fruit); corollas glabrous, cleft below the middle, the throat flaring, the lobes spreading; fruit hairs abundant, short, stout.

Moist ledges and shady woods along stream banks and springs; 1800–2400 m. Del Carmen Mountains, Coahuila; Chisos Mountains, Brewster Co., and Davis Mountains, Jeff Davis Co., Texas. Although there is some uncertainty about the situation in Jeff Davis Co., the new subspecies appears to be allopatric to the other subspecies.

This taxon includes all collections from the Big Bend region of Texas and Coahuila and a few collections from Jeff Davis Co. (the latter all from "upper Limpia Canyon", *E. J. Palmer 30698, 30807, 34366*). Although the general appearance of the plants, with slender flaccid leaves and long capillary pedicels, is precisely that of *G. concinnum* T. & G. from the eastern and middle western United States, it differs significantly in having fruits with curved or hooked hairs and in the more definitely

campanulate corollas. One is tempted to interpret it as being of hybrid origin, an interpretation nicely supported by the orientation of the marginal hairs on the leaves. *Galium mexicanum* in general has usually many stout retrorse prickles on the leaf margins. In *G. concinnum,* however, although the leaves are nearly glabrous, such hairs as can be found are antrorse. In *G. mexicanum* ssp. *flexicum,* the situation is intermediate, the relatively slender hairs on the basal half of the leaf being basally directed, and those on the apical portion being apically directed. The presence of hairs on the ovaries is considered to be critical in assigning ssp. *flexicum* to *G. mexicanum* rather than to *G. concinnum.*

The Palmer collections from the Limpia Canyon, Jeff Davis Co., differ from those of the Del Carmen and Chisos mountains only in that the marginal leaf-hairs are a little stouter and all basally directed. On the other hand, they differ sharply from plants of Mt. Livermore and elsewhere in the Davis Mountains, all of which are clearly ssp. *mexicanum.*

I thank Rimo Bacigalupi for editing the Latin.

VEGETATION SURROUNDING KINGS LAKE BOG, WASHINGTON

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This communication describes vegetation surrounding a small bog lake in lowland King County, Washington. We tested the hypothesis that the plants comprising vegetation surrounding this bog are arranged in zones rather than continuously in response to environmental gradients.

Vegetation can be analyzed by two distinct approaches. Numerical classification methods group samples into categories and emphasize similarities within and differences between categories. Ordination methods arrange samples sequentially based on environmental data or on compositional similarity of the vegetation itself or both. Both methods can contribute to the understanding of vegetation and the causes of vegetation organization.

Gauch and Whittaker (1972) documented the growing realization of many ecologists that simple geometric ordinations are superior to more elegant methods in several ways. They are mathematically straightforward and the results are usually more reliable. Ordination approaches have been successfully applied to many situations but seem best adapted to those in which beta diversity is low and vegetation scale being investigated is intermediate (Gauch, 1973).

Vegetation classification has a venerable history with many "traditions" (Shimwell, 1973; Mueller-Dombois and Ellenberg, 1974) that will not be reviewed here. We favor methods that emphasize dominants rather than differential or character species. We selected an agglomerative hierarchical method devised by Orloci (1969) based on comparisons of information gained when two groups are merged and that produces a dendrogram. This method is superior to non-hierarchical numerical classification methods (Williams, 1971).

All hierarchical classifications are plagued by the problem of termination; analysis proceeds until all samples are placed into a single group. The investigator must intuitively determine when joining groups should cease. Del Moral (1975) proposed a solution to this problem by using stepwise discriminant analysis. Clustering terminates when as many or more groups are recognized by the classification as are tentatively thought to occur in the field. Discriminant analysis assesses statistical differences between groups, reallocates individual samples if necessary, and indicates the relative importance of species in constructing the classification.

Kings Lake Bog lies in the western foothills of the Cascade Mountains (N47°35′40″, W 121°46′35″), at 280 m, well within the *Tsuga heterophylla* zone in the Puget Trough (Franklin and Dyrness, 1973). Kings Lake is 1.1 ha and is surrounded by a 21 ha bog. It is 4.6 m deep off the mat edge (Wolcott, 1973). The surrounding forest was logged and burned in the 1930's by the Weyerhaeuser Company, upon whose land the lake is located (Fitzgerald, 1966).

The area we sampled extends from the floating mat edge to a portion of the surrounding forest (fig. 1). A lagg (Oswald, 1933) borders the east and southeast lakeside; it is covered by fallen logs and abruptly joins higher ground. *Spiraea douglasii* occupies much of this area. The remaining sides of the bog exhibit a more gradual change in forest and our sample was confined to this zone of transition.

Fitzgerald (1966) showed that the microclimate of the open bog was more extreme than that of the surrounding forest. Temperature extremes varied annually from 43° C to − 17° C on the bog and from 21° to 6° C in the forest. Diurnal variation, due to more insolation and intense reradiation, was much greater on the bog than in the forest. For example, in one 24 hr period in July, 1965, temperature varied 20° C on the bog compared to 6° C in the forest. The bog experiences many more days of sub-freezing temperature than the surrounding forest. The water table fluctuates such that during early spring, standing water may be found above the moss layer throughout the bog while in late summer the mat is very dry. By these climatic criteria, the bog habitat is more severe than the forest.

Methods

Vegetation sampling. We sampled vegetation along a 216 m by 10 cm line intercept transect from the mat edge into forest. Within alternate

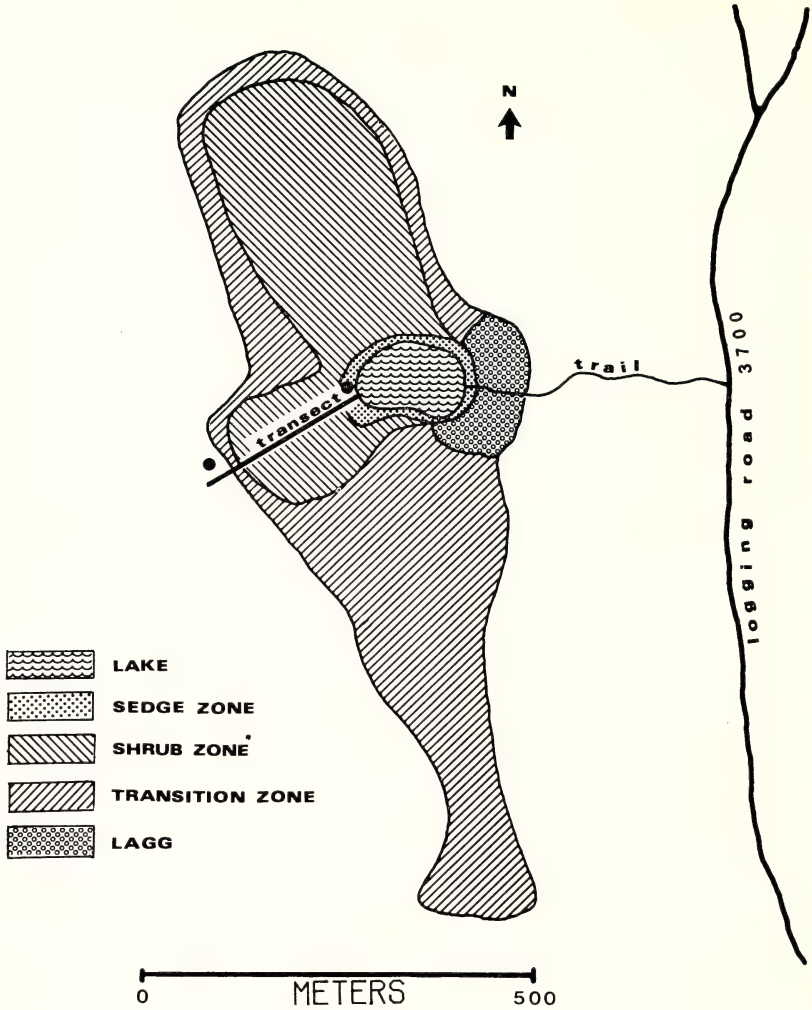

FIG. 1. Vegetation zone map of Kings Lake Bog showing location of access trail and transect. Forest is unshaded.

1 m segments, we recorded leaf intercept at each centimeter. The bog contains hummocks between the forest and the floating mat. In order to reduce sampling errors inherent in such heterogeneous communities, cover was expressed as the percentage of centimeter occurrences per meter. We did this because we were not interested in microtopographic patterns, which we observed on a scale of a few centimeters. Sampling error is fairly high for rare species but lower for common species. A preliminary study compared 1 m^2 quadrats with line intercept values and

gave similar results (means and standard deviations). The analyses reported here are confined to 14 more common species.

Quantitative analysis. Percent cover for the 14 dominant species was used in our analyses. Orloci's (1969) mutual information method was implemented with a computer program modified from Goldstein and Grigal (1971). The matrix is inspected for local minima and the corresponding subsets are united to form new groups with minimum information gain. The results are displayed by a dendrogram that shows the mutual information at which each subset is joined.

Once tentative groups are identified tests of significance of group differences and tests of group membership are accomplished with stepwise multiple discriminant analysis (SMDA). Mathematical details are found in del Moral (1975), who followed Dixon (1970). Given a partitioned set of data, SMDA determines the order in which variables (species) are useful to distinguish between groups. At each successive step an F-test for differences between groups is made. Individual samples are evaluated to determine the class to which they belong. This permits an *a posteriori,* objective, reallocation of the samples. The phytosociological relationships among the groups are determined by means of canonical rotation of the discriminant axes. What results is a set of mutually orthogonal (independent) axes in which variation is maximized on the first axis. Samples are plotted according to the first two canonical axes, thus providing an optimum two-dimensional picture of the relationships between groups.

We also used similarity projection ordination (Gauch and Whittaker, 1972) to determine vegetational relationships. This is a multidimensional extension of the polar ordination method of Bray and Curtis (1957). To effect an ordination, we selected two samples that contrasted strongly. Several trials, based on the similarity matrix, were used. We selected an internal association of 90 percent arbitrarily since a) published values vary from 80 to 100 percent and b) Gauch and Whittaker (1972) concluded that internal association has little effect on rank order in ordinations. All other samples are projected orthogonally onto the axis defined by the end stands. A second axis was defined by stands chosen with the following criteria: stands from the center of the first axis, stands quite dissimilar to each other, and stands distinct from the first axis. Additional dimensions did not improve the ordination.

Results and Discussion

Qualitative Description. Prior to selection of transect location, a general survey was made. Fitzgerald (1966) divided this bog subjectively into five zones. We added the lagg area and classified samples of vegetation into one of the six zones and recorded species composition. Table 1 provides a qualitative list of species encountered in each zone. Nomenclature of vascular plants follows Hitchcock and Cronquist (1973), moss nomenclature follows Lawton (1971), and lichen nomenclature follows Hale (1969).

TABLE 1. OCCURRENCES OF ALL TAXA ENCOUNTERED IN SIX ZONES AROUND KINGS BOG. F = forest, T = transition zone, S = shrub zone, Se = sedge zone, L = lagg, P = pioneer zone. Species used in quantitative analysis are marked *.

	Vegetation zone					
Taxon	F	T	S	Se	L	P
*Tsuga heterophylla	X	X	X		X	X
Thuja plicata	X	X	X		X	
Picea sitchensis	X				X	
Pseudotsuga menziesii	X				X	
Acer circinatum	X				X	
*Ledum groenlandicum		X	X		X	X
*Kalmia occidentalis		X	X		X	X
*Vaccinium oxycoccus		X	X	X	X	X
Vaccinium alaskense	X	X	X		X	
Vaccinium ovalifolium	X	X			X	
Vaccinium parvifolium	X				X	
Spiraea douglasii		X			X	
*Gaultheria shallon	X	X	X			
Menziesia ferruginea	X					
Rubus spectabilis	X					
Sambucus racemosa	X					
Symphoricarpos occidentalis					X	X
Maianthemum dilatatum	X	X			X	
*Cornus canadensis	X	X			X	
Pyrola uniflora	X					
Circaea alpina	X					
Montia sibirica	X					
Galium aparine var. echinospermum	X					
Actaea rubra	X					
Corallorhiza sp.	X					
Listera sp.	X					
Lycopodium annotinum	X					
*Pteridium aquilinum var. pubescens	X	X	X			
Trientalis arctica					X	
Agrostis oregonensis					X	
Potentilla palustris					X	X
Nuphar polysepalum			X		X	
Menyanthes trifoliata				X	X	X
Drosera rotundifolia				X		X
Carex cusickii			X	X		X
Carex vesicaria			X	X		X
Juncus ensifolius			X	X		X
Juncus effusus var. compactus			X	X		X
*Rhynchospora alba				X		X
Cicuta douglasii						X
Lysichitum americanum		X	X	X	X	
Polysticum munitum	X					
*Cladonia rangiferina			X	X		
Usnea longissima	X	X	X		X	
*Sphagnum subsecundum		X	X	X	X	X
*Pleurozium schreberi		X	X		X	
Rhytidiadelphus triquetrus	X		X			
Aulacomnium androgyne	X		X			
Polytrichum juniperinum	X		X			

TABLE 1. *Continued.*

*Hylocomnium splendens	X	X				
*Eurhynchium praelongum var. stokesii	X					
Isothecium stoloniferum	X					
Dicranum sp.	X					
Bryum sp.	X					
Total numbers	33	17	21	11	24	15

Each vegetation zone is recognized by both dominants and physiognomy. Aspect zonation around the lake is clear. At the edge of the sphagnum mat is a peat-sedge zone in which dominance is shared by *Rhynchospora alba, Vaccinium oxycoccus,* and *Cladonia rangiferina.* A shrub zone dominated by *Ledum groenlandicum, Kalmia occidentalis,* and stunted *Tsuga heterophylla* borders the first zone. This mounded zone is heterogeneous with mounds and intermounds having different species composition. Intermounds are dominated by *Sphagnum subsecundum* and *Pleurozium schreberi.* The forest proper rises abruptly from the edge of the shrub zone.

Closer inspection reveals additional distinct areas. Between the sedge zone and the lake lies a very narrow band consisting of two phases and termed the pioneer zone: *Ledum groenlandicum, Kalmia occidentalis,* and *Potentilla palustris* form a matrix extending into the lake. Within this matrix may be found *Sphagnum subsecundum* and *Drosera rotundifolia.*

Within the sedge-peat zone, considerable seasonal variation in aspect dominance occurs. *Rhynchospora* dies back to an underground rhizome annually. *Cladonia* is sporadic. While numerous, *Vaccinium oxycoccus* has low cover. All of these are obscured by *Rhynchospora* during spring and summer.

The shrub zone maintains its appearance throughout the year since the dominants are evergreen and form a dense intertwined layer. The mat layer beneath the shrubs consists of *Vaccinium oxycoccus, Sphagnum subsecundum, Cladonia rangiferina,* and *Pleurozium schreberi.* Punctuating this mat are sporadic *Lysichitum americanum* individuals in depressions. Pools of various sizes also occur and are dominated by *Juncus effusus, J. ensifolius* var. *compactus, Carex cusickii,* and *C. versicaria,* all of which also occur in the sedge zone. (These pools were not sampled by the intercept transect.)

The forest shrub transition zone is an interdigitation of forest and shrub zone species. *Pteridium aquilinum* var. *pubescens* and *Gaultheria shallon* extend farther into the shrub zone than other forest species. *Vaccinium alaskense* and then *V. ovalifolium* are encountered as the hemlocks gain stature. *Cladonia rangiferina* and *V. oxycoccus* are the first bog species to disappear. *Sphagnum subsecundum* and *Pleurozium schreberi* are replaced gradually by *Hylocomnium splendens, Eurynchium*

praelongum, and *Rhytidiadelphus triquestrus.* Within the forest, the terrain is level and species common to *Tsuga heterophylla* forests occur (Table 1).

The lagg is a special type of vegetation that does not extend completely around the bog. It is richer in species than all but the forest zone. *Spiraea douglasii, Lysichitum americanum,* and *Symphoricarpos occidentalis* are among the common species.

While most species on the bog display regular patterns with respect to the major environmental gradients associated with the degree of "bogginess", some occur sporadically in response to the presence of water pools.

Lysichitum americanum is sporadic throughout the bog from mat edge to forest margin. Turesson (1916) believed that *Lysichitum* was relictual, maintaining itself by shading and mechanically destroying *Sphagnum,* the main invader. Each individual *Lysichitum* is rooted in a deep hollow, the edges of which may be lined with forest moss species such as *Aulacomnium androgyne, Rhytidiadelphus triquetrus,* or *Polytrichum juniperinum.* Turesson's hypothesis does not explain the presence of *Lysichitum* in the hanging mat.

Many individuals of *Lysichitum* are found in the lagg, which is similar to its usual swampy habitat. Pools may be formed in the mat by various disturbances, including wind throw of adjacent trees and trampling by man or beast. These pools may be invaded and enlarged by *Lysichitum.* Therefore, we believe that *Lysichitum* invades disturbed bogs. Its density is being monitored annually to test this hypothesis.

Other species occur in atypical patterns in this bog. Most patterns are due to the presence of the lagg or to downed timber creating less boggy conditions and variable seed beds. Species such as *Nuphar polysepalum* and *Menyanthes trifoliata* occur in pools in the mat even though these are usually considered lake margin species. Where fallen logs occur, forest understory species invade to the edge of the lake. Thus *Vaccinium parvifolium, Cornus canadensis,* and *Maianthemum dilatatum* occur on rotting logs at lake margin. These species often occur on fallen logs in the forest and such a distribution is not surprising.

Zones viewed on the basis of dominant species are identified in the field. However, our fundamental question is not whether zones can be distinguished subjectively. Several generations of ecologists have demonstrated that this is possible and useful. We wished to determine if such subjective zones maintain their discreteness in the face of an objective analysis.

Quantitative Description. The location of the transect with respect to a vegetation map of Kings Lake Bog, which emphasizes zonation, is shown in Figure 1.

Dendrogram. We clustered 108 samples by MINFO (Goldstein and Grigal, 1971). The dendrogram (fig. 2) confirms the validity of the zonation concept when dealing with dominant vegetation. Sample numbers across the bottom of Figure 2 are the sequence in which samples

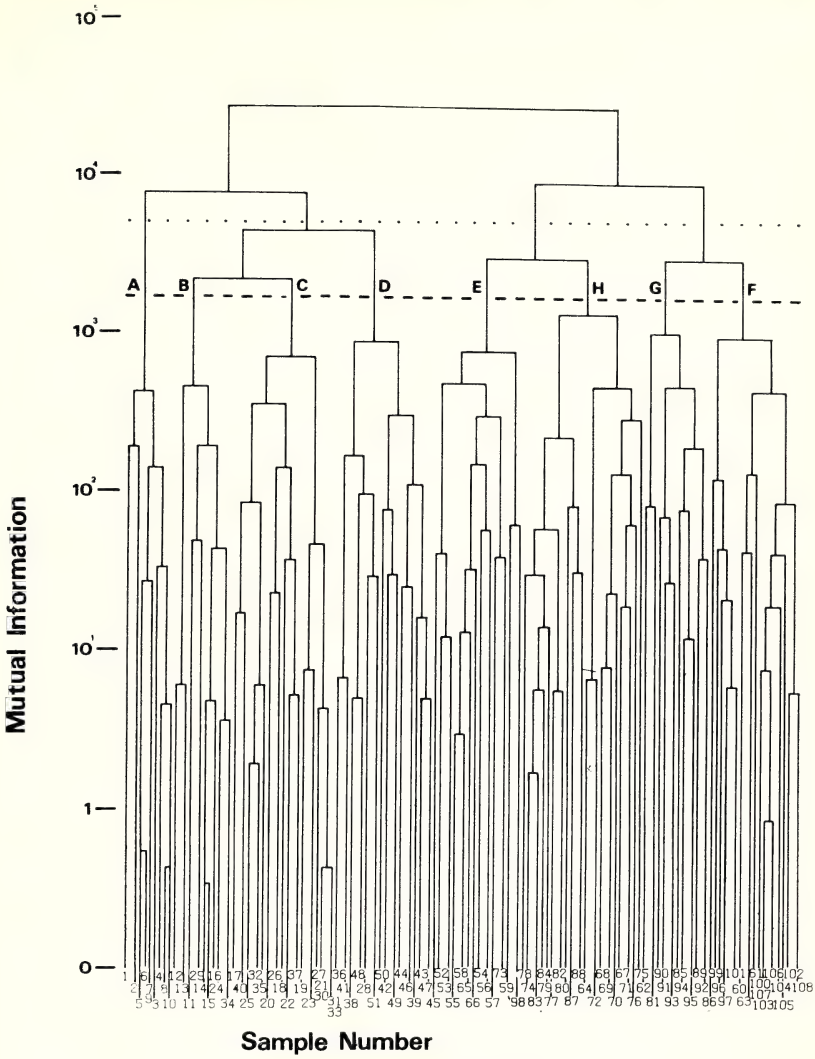

FIG. 2. Dendrogram produced by MINFO. Letters indicate the eight groups used in subsequent analyses. The dotted line (5×10^3) indicates the level of similarity required to produce four zones. Sample numbers are sequence in the transect.

were encountered from the Lake to the forest. If clustering is terminated at the 5×10^3 level of mutual information (dotted line), then four groups, corresponding to the sedge zone, the shrub zone, the transition, and the forest, are recognized. Termination at 2×10^3 (dashed line) results in the eight groups labeled in Figure 2. Some features not ordinarily noted in dendrograms emerge from a consideration of this one. In the

dendrogram, sample similarity is indicated by the level of first joining. The degree of sample similarity appears highest in the sedge zone, least in the transition, and intermediate in the others. Thus, the dendrogram produces classes but simultaneously differential relationships between samples imply a gradational pattern.

Discriminant analysis. The eight subsets were investigated by stepwise discriminant analysis to determine whether any samples should be reallocated, to determine whether any pair of clusters should be merged, to determine the relationship of the groups to each other, and to determine the relative importance of species. In Table 2 we list the order in which species were used to distinguish among the classes. The two most important species distinguished between forest and sedge zones, the third is primarily a shrub zone species, and the fourth is a transition zone species.

After 14 steps, the eight groups are all highly statistically significantly different ($P < 0.01$, d.f. = 14, 87). Six samples are reallocated by this analysis, four transferring samples from C to B. The final F-table (Table 3) indicates that clusters B, C, and D are closely related. These three are united by *Ledum* dominance, but D has high cover of *Pleurozium schreberi,* while B and C are distinguished on the basis of *Vaccinium oxycoccus.* Cluster A can be recognized by dominance by *Rhynchospora* and *Cladonia.* Clusters F, G, H, and E belong to the forest and transition. Clusters E and H are related on the basis of *Pleurozium* and *Ledum.* Cluster F is distinguished by high concentrations of *Hylocomnium* and *Pteridium,* while G is a mixture dominated by *Pteridium.* Cluster H lacks *Tsuga* and is characterized by *Pteridium, Pleurozium,* and *Ledum,* while E is dominated by *Gaultheria, Ledum,* and *Pleurozium.* The den-

TABLE 2. RANK ORDER OF SPECIES DETERMINED BY DISCRIMINANT ANALYSIS. F-value indicates the relative information and degree of significance with 7 and 87 degrees of freedom.

Step Number	Species	F-valule	P of Larger F-value
1	Hylocomnium splendens	130.5	0.005
2	Rhynchospora alba	111.9	0.005
3	Kalmia occidentalis	65.7	0.005
4	Pleurozium schreberi	24.1	0.005
5	Cladonia rangiferina	13.5	0.005
6	Gaultheria shallon	12.7	0.005
7	Ledum groenlandicum	15.7	0.005
8	Pteridium aquilinum	8.1	0.005
9	Sphagnum subsecundum	6.9	0.005
10	Eurhynchium praelongum	4.4	0.005
11	Maianthemum dilatatum	2.3	0.05
12	Vaccinium oxycoccus	2.3	0.05
13	Cornus canadensis	1.3	n.s.
14	Tsuga heterophylla	1.0	n.s.

TABLE 3. F-VALUES BETWEEN PAIRS OF GROUPS (see fig. 2). Degrees of freedom = 14, 87. Values exceeding F = 2.28 occur between two sets of samples from the same group with P < 0.01.

A							
46.885	B						
61.448	6.663	C					
63.061	10.438	6.877	D				
60.626	20.405	24.163	17.483	E			
78.285	54.639	72.073	72.591	49.955	F		
38.051	27.907	32.868	34.340	29.836	24.937	G	
59.262	25.696	27.919	25.254	12.389	55.365	19.449	H

drogram tends to confirm the impressions produced by the F-table. Here, A joins B, C, and D at a high level of information. B and C are closely related and D is more closely related to these than to others. The affinity of E and H is demonstrated as is that of F and G. E is intermediate between H and D and closer to H by F-test as is confirmed by the dendrogram.

Discriminant analysis includes a determination of canonical axes. The first canonical axis accounts for 41.7 percent of the variation while the second accounts for 21.2 percent; both axes have high correlation with the discriminant axes. Figure 3 is a two dimensional plot of the canonical distribution of samples. This plot reconfirms our conclusions concerning the relationships among the eight groups. B, C, and D are shown to be closely related, E and H are relatively close, F and G are more distinct and A is very distinct. A, F, and G are all loosely defined groups. Group A is in the sedge zone and F is in the forest zone, suggesting that some rotation of these axes represents an approximation of the original transect that is a gradient of nutrient availability and soil oxygen content (Lebednik, unpublished).

Key to Vegetation Clusters. The discriminant analysis provides information to produce a key to the vegetation types recognized. Our key uses those species highest in the rank order of information. In Table 4 we list the composition of the eight groups according to the zonation perceived subjectively. The following key may be used to identify these types in the field:

a. *Rhynchospora alba* dominant (Sedge Zone) . . . . . Type A
aa. *Rhyncospora alba* rare or absent, Ericaceous shrubs common
  b. *Kalmia occidentalis* dominant (Shrub Zone)
    c. *Pleurozium schreberi* over 25% cover . . . . . Type D
    cc. *Pleurozium schreberi* rare or absent
      d. *Sphagnum subsecundum* common . . . . . Type C
      dd. *Sphagnum subsecundum* absent, *Cladonia rangiferina* common . . . . . Type B

bb. *Kalmia occidentalis* rare or absent
  e. *Pleurozium schreberi* over 50%, or if less, then *Ledum groenlandicum* common (Transition zone)
    f. *Pteridium aquilinum* common . . . . . Type H
    ff. *Pteridium aquilinum* rare . . . . . Type E
  ee. Both *Pleurozium schreberi* and *Ledum groenlandicum* rare (Forest Zone)
    g. *Gaultheria shallon* and *Hylocomnium splendens* common . . . . . Type F
    gg. *Pteridium aquilinum* dominant, others mixed . . Type G

Similarity Projection Ordination. The dendrogram suggests greater continuity in the data than is manifest by classification approaches. Simi-

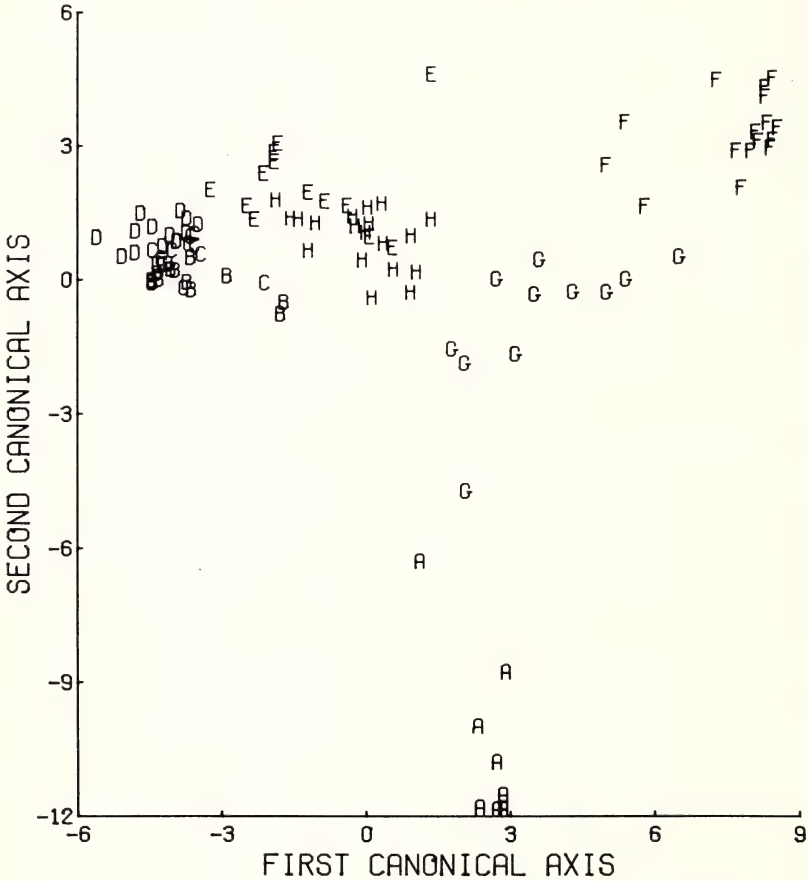

FIG. 3. Canonical distribution of the eight groups determined by discriminant analysis. Letters refer to groups in Figure 2.

TABLE 4. MEAN COVER PERCENTAGE OF DOMINANT SPECIES FOR THE EIGHT REVISED GROUPS IDENTIFIED IN MINFO.

Taxon	Cluster								Transect
	A	B	C	D	E	F	G	H	Mean
Ledum groenlandicum	1.0	99.2	97.6	99.2	67.3	4.2	4.0	41.8	53.0
Kalmia occidentalis	4.9	85.0	90.3	84.6	6.2	0.9	0.0	5.6	34.2
Vaccinium oxycoccus	15.2	5.0	65.6	50.4	0.0	0.0	0.0	0.0	18.6
Rhynchospora alba	80.3	0.0	0.1	0.0	0.0	0.0	0.0	0.0	7.4
Sphagnum subsecundum	0.0	0.0	58.2	8.6	2.3	5.0	1.0	28.9	16.5
Pleurozium schreberi	0.0	4.9	0.0	75.6	78.8	2.5	14.0	65.3	32.8
Cladonia rangiferina	38.0	78.0	12.8	5.0	0.8	0.0	0.0	0.0	13.3
Tsuga heterophylla	0.0	23.3	3.6	15.0	0.8	0.9	13.5	0.0	5.8
Gaultheria shallon	0.0	0.0	0.0	3.2	77.3	73.7	14.0	49.5	30.6
Pteridium aquilinum var. pubescens	0.0	0.0	0.0	0.2	5.2	22.8	64.0	77.6	23.6
Hylocomnium splendens	0.0	0.0	0.0	0.0	5.8	92.5	22.0	0.8	16.8
Eurhynchium praelongum	0.0	0.0	0.0	0.0	0.0	0.3	21.5	0.0	2.0
Cornus canadensis	0.0	0.0	0.0	0.0	3.8	3.8	4.0	0.3	1.4
Maianthemum dilatatum	0.0	0.0	0.0	0.0	0.0	0.3	3.0	0.0	0.3

larity projection ordination was used to determine whether a continuum approach recognizes the community types reported above.

The first axis is defined by samples 32 (a member of group C) and 97 (group F) and the second axis is defined by samples 10 (group A) and 67 (group H). The first axis represents shifts within shrub dominated vegetation and the second in non-woody dominated vegetation. The resultant ordination is shown in Figure 4, in which previously recognized communities are circumscribed. The rate of change of species (beta diversity) along the first projection axis is relatively large so that there is distortion of the type reported by Gauch (1973) in his analysis of Bray-Curtis polar ordination, to which Similarity Projection Ordination is closely related. Samples toward the middle of the first projection axis tend to be distant from it so that there is a "hump" in the analysis. This hump results because Percent Distance is not a linear estimator of ecological relationships between the samples.

Ordination suggests that, with the exception of type A, the *Rhynchospora* dominated community, the data are continuous. The *Rhynchospora* community is unique by virtue of the virtual absence of erect shrubs. Communities B, C, and D, which are closely related in the classification hierarchy, are likewise clustered in the ordination and linked by cover of *Ledum* and *Kalmia*. Communities F (*Gaultheria/Hylocomnium*) and G (*Pteridium/Hylocomnium-Eurhynchium*) are distinct (except for sample 93) and can correctly, if arbitrarily, be separated from each other and from E (*Gaultheria/Pleurozium*) and H (*Pteridium-Gaultheria/Pleurozium*). However, communities E and H, which are as

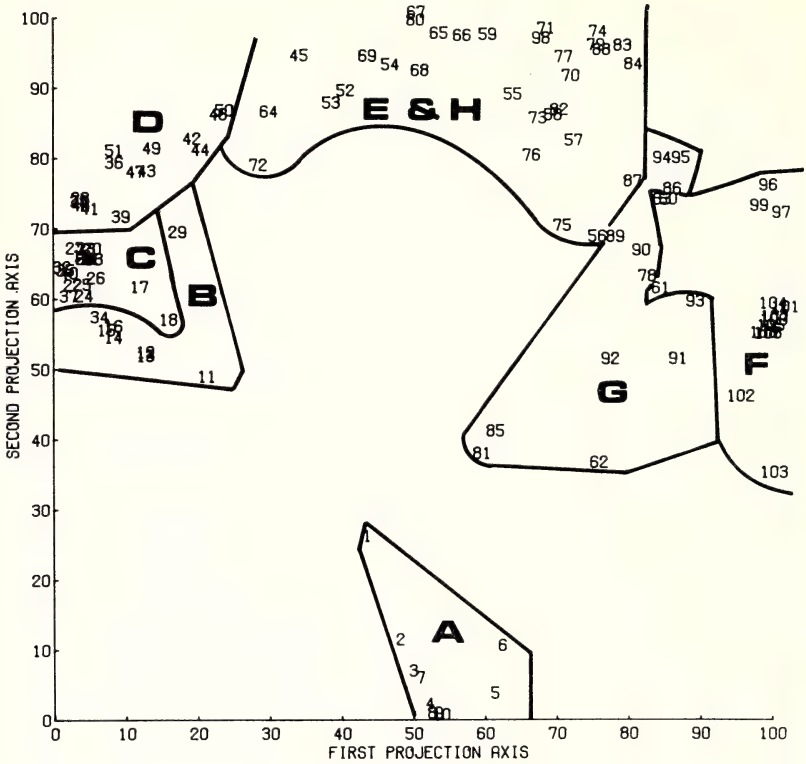

FIG. 4. Similarity projection ordination using samples 32 and 97 as end points for the first axis and samples 10 and 67 for the second. Samples representing the eight groups revealed by MINFO (A–H, see fig. 2) are circumscribed.

related to each other as are F and G, are scrambled in the middle of axis one at the upper end of axis two. These samples occur in a transition zone, show little tendency to cluster, are well separated from other samples, and are intermixed. The ordination reflects the classification better at the four group level than at the eight group level.

Although similarity projection and discriminant analysis are entirely different analytical tools, they produce similar results (cf. figs. 3 and 4). All groups occupy similar relative positions though spacing is distorted due to different mathematical assumptions. Community type G is plotted lower on the second canonical axis in relation to F than in similarity projection. In both, the integradation of E and H is evident though it is more pronounced in the similarity projection.

Comparison of Classification and Ordination. The two approaches of this study reveal that while the vegetation can be treated as four vegetation zones, the continuum approach suggests the gradient nature of the vegetation. The vegetation may be classified numerically by a method

that stresses dominance types, and the resultant classes can be recognized in an ordination. However, canonical analysis of these types reveals considerable variation within a type and continuity between seven of the eight types. Since we obtained this result with only 14 common species, we believe that this conclusion applies even more strongly to cases of greater species richness.

Fitzgerald (1966) studied this bog by means of relevés in the style of Braun-Blanquét. She discerned the four zones we have retained in our discussions. Our methods suggest that greater complexity of community pattern exists. They also recognize that the classes, with one exception, are arbitrary modes in an essentially continuous pattern.

Conclusions and Summary

The vegetation of Kings Lake Bog has been described by classification and ordination methods. The question posed by this study was whether vegetation forms distinct zones around this bog or whether it forms a continuous pattern. Combined analyses suggest that vegetation forms a gradient except for one distinct type, distinguished by *Rhynchospora alba* and several other sedge species. This type occurs on the most exposed portion of the floating mat where woody ericacous shrubs have not invaded. Zones may be recognized in the remaining portions of the gradient from lake to forest, but these zones reflect only the distribution of dominant species. Our classification constructed more communities than were recognized by Fitzgerald (1966) and discriminant analysis suggests that these form a nearly continuous sequence.

The combined use of classification and ordination methods in this study reveals a correlation between philosophically contrasting approaches. The similarity between canonical distribution of samples and similarity projection analysis is striking when one considers the disparate mathematical approaches. For mapping and synthesis of vegetation data, we recommend numerical classification methods such as MINFO. The use of discriminant analysis to refine resultant classifications provides a means for objective reallocation of samples and for assessing the validity of each group. Where the behavior of individual species is important, then ordination methods are superior. Ordinations may be divided into segments for ease of consideration, but we propose that such partitioning be done on the basis of numerical classification methods.

Acknowledgments

We are indebted to A. R. Kruckeberg, M. F. Denton, and P. A. Lebednik, who each made valuable contributions to the paper. Funds were provided by the Department of Botany, University of Washington, and by the College of Arts and Sciences, University of Washington. The Weyerhaeuser Company permitted this study to be carried out on a portion of their Snoqualmie Tree Farm.

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NOTES AND NEWS

FLY POLLINATION OF PENSTEMON DAVIDSONII AND P. PROCERUS (SCROPHULARIACEAE).—Agents implicated as pollinators of various species of *Penstemon* include: hummingbirds, coleopterans, carpenter bees, honeybees, bumblebees, solitary bees, masarid wasps, bee flies, syrphid flies, moths, and many other hymenopterans, dipterans, and lepidopterans (references below and: Clements and Long, Publ. Carnegie Inst. Wash. 336, 1923; Cooper, Amer. Midl. Naturalist 48:103–110, 1952; Merritt, Erythea 5:15–22, 1897; Robertson, Trans. Acad. Sci. St. Louis 25:277–324, 1927, *Flowers and insects,* 1928; Straw, Evolution 9:441–444, 1955 Amer. Naturalist 90:47–53, 1956). Heretofore, fly pollination of *Penstemon* has been described in

detail only by Straw (Ecology 44:818–819, 1963), although there are many incidental citations, especially in the older literature (see Knuth, *Handbuch der Blütenbiologie,* Bd. 3, Tl. 2, 1905, *Handbook of flower pollination,* Vol. 3, 1909). The purpose of the present note is to extend records on pollination of *Penstemon* to an additional species, *P. procerus* Dougl. ex Grah., and for this species and *P. davidsonii* Greene ssp. *davidsonii* (vouchers in UC as *Schmid 1975–21* and *1975–20,* respectively), also to a new geographic region (Oregon). Pollination by bees (Knuth, op. cit., 1905, for cultivars in Europe) has been reported for *P. menziesii* Hook. [a nomenclaturally illegitimate name relegated to the synonymy of *P. davidsonii* as ssp. *menziesii* Keck (Keck and Cronquist, Brittonia 8:247–250, 1957)], whereas pollination by bumblebees (Baker and Baker, New Phytol. 76:87–98, 1976) and hummingbirds (Grant and Grant, *Hummingbirds and their flowers,* 1968) has been reported for *P. davidsonii* ssp. *davidsonii* [= *P. menziesii* Hook. ssp. *davidsonii* (Greene) Pennell].

The flies (specimens deposited in UC Berkeley Insect Collection) observed visiting flowers of *Penstemon* were *Allograpta* sp. (Syrphidae) on *P. procerus* (fig. 1) and

FIG. 1 A syrphid fly (*Allograpta* sp.) visiting *Penstemon procerus.*

Hylemya alcathoe Walker (Anthomyiidae) and *Hilara* sp. (Empididae) on *P. davidsonii.* Both plant species were growing in profusion along Highway 242, about 2 km west of McKenzie Pass, 1624 m, Deschutes Co., Oregon. Activities of the insects conformed in general to observations of previous workers (references above and below) on other species of *Penstemon.* Each fly spent several minutes either on or, especially, in a flower, and each also visited successively several flowers of a species. This mode of operation of the insects presumably would be adequate for cross-pollination (data on xenogamy versus geitonogamy were not collected). Since *P. davidsonii* has both stamens and style included, an insect must completely enter the corolla tube to effect pollination. No insects other than flies were sighted on the flowers during my observations, which were made in late afternoon of 20 Aug 1975.

The syrphid flies ate pollen and seemed to take nectar from the flowers. The latter was not actually seen since the nectariferous hairs are concealed within the tubular corolla, being borne on the bases of the upper pair of stamens (Straw, Phytomorphology 6:112–119, 1956, Brittonia 18:80–95, 1966). In addition, the syrphid flies apparently glean stray pollen from the lower lip of *Penstemon procerus,* a procedure also observed by Crosswhite and Crosswhite (Amer. Midl. Naturalist 76:450–467, 1966) for syrphids visiting other species of the genus. Syrphids, it might be noted, have been observed taking both nectar and especially pollen from flowers of many other plant families (Schmid, Principes 14:39–49, 1970).

I thank L. R. Heckard, P. F. Yorks, and E. I. Schlinger for identifying plants and/or insects; Tom DeCew provided field assistance.—RUDOLF SCHMID, Department of Botany, University of California, Berkeley 94720.

Range Extensions of Three Conifers and a Dwarf Mistletoe in the Panamint Mountains, Death Valley National Monument.—The ranges of three conifers, *Pinus aristata* Engelm. (syn. *P. longaeva* D. K. Bailey) (*Johnson 73311–1,* IFGP), *P. flexilis* James (*Johnson 73311–3,* IFGP), and *Juniperus occidentalis* Hook. (*Johnson 73311–5,* IFGP), extend farther south in the Panamint Mountains than heretofore reported by Griffin and Critchfield (*The distribution of forest trees in California,* USDA Forest Serv. Res. Pap. PSW-82. 1972). On 7 Nov 1973, I climbed Sentinel Peak (2937 m) by way of Panamint Pass. I was investigating a report that *P. jeffreyi* Grev. & Balf. grew on the southwest slope of the peak in the Panamint Range on the western border of Death Valley National Monument. I did not find *P. jeffreyi* but extended the range for the three conifers to Sentinel Peak, which is 8.2 km south of the well-known bristlecone pine stand on Telescope Peak (3368 m). Sentinel Peak's climbing register shows that the mountain has often been climbed. And yet the occurrence of bristlecone pine—an easily recognized and highly publicized species—has until now gone unreported for this desert peak. While on a second expedition to the Panamint Range in April 1975, I found a further extension of *P. flexilis* (*Johnson 75116–1,* IFGP) to Porter Peak (2774 m), 5.5 km south of Sentinel Peak.

Death Valley and vicinity have been repeatedly "botanized". The earliest comprehensive botanical reconnaissance of this area was the U. S. Department of Agriculture's Division of Botany biological survey in 1891 (Coville, Contr. U.S. Natl. Herb. 4:1–363. 1893; Merriam, North American Fauna 7:285–343. 1893). The expedition collected bristlecone pine on Telescope and White Mountain Peaks in California and on Charleston Peak, Nevada. In February 1891, Coville (op. cit.) and Funston crossed the Panamint Mountains in a "terrific snowstorm". They were within sight of the Sentinel Peak bristlecone pine stand but were apparently more concerned with their own survival than with observing plants. They crossed Panamint Pass in late February 1891, but a heavy snowpack may have prevented their scouting the area south of the pass. In March 1891, a reconnaissance party of the expedition made a base camp in Johnson Canyon just east of Sentinel Peak and ". . . excursions were made to various adjacent points". Even though they were camping in the shadow of Sentinel Peak, they did not detect the bristlecone pine stand.

The published distribution of bristlecone pine in the Death Valley area is confusing. Sudworth (*Forest trees of the Pacific slope,* 1908) reported bristlecone pine in the Panamint Range and later (*Geographic distribution of North American trees, Part I, pines,* 1913) mapped the Telescope Peak stand as the only grove on the mountains surrounding Death Valley. Subsequently, Sudworth (*The pine trees of the Rocky Mountain region,* 1917) added locations in the Cottonwood, Grapevine and Funeral Mountains. His original worksheet map (on file at the Pacific Southwest Forest and Range Experiment Station, Berkeley, California) shows that these range extensions are based on "Information furnished by District No. 5 [of the U. S. Forest Service]". According to Peter G. Sanchez, resource management specialist, Death Valley National Monument (pers. comm., June 1975), bristlecone pine has not been collected or found in the Cottonwood, Grapevine, or Funeral Mountains. Therefore, the information furnished by District No. 5 has never been corroborated.

Munns (*The distribution of important forest trees of the United States,* 1938) repeated the errors in his map book. Munz (*A California flora,* 1959, and *A flora of southern California,* 1974) perpetuated the report of bristlecone pine growing in the Grapevine and Funeral Mountains. Miller (Ecology 27:54–60. 1946) climbed Grapevine (2663 m) and Wahguyhe (2630 m) Peaks in the Grapevine Mountains, Nevada, and surveyed the surrounding area. He reported *Pinus flexilis* and *P. monophylla* Torr. & Frem. growing on these peaks. Miller thus confirmed the findings of Coville (op. cit.), who reported discovering *P. flexilis* on Grapevine Peak in 1891.

On Sentinel Peak, bristlecone pine grows in association with *Pinus flexilis, P. monphylla, Juniperus occidentalis,* and *J. osteosperma* (Torr.) Little, mainly above 2800 m.

The *Pinus flexilis* on Porter Peak is confined to the west, northwest, and northeast slopes, generally above 2560 m. A dwarf mistletoe was collected on *P. flexilis* on the northwest slope of Porter Peak and sent to Dr. Frank G. Hawksworth, U. S. Forest Service, Fort Collins, Colorado, for identification. Dr. Hawksworth (pers. comm., May 1975) identified the dwarf mistletoe as *Arceuthobium cyanocarpum* Coulter & Nelson (*Johnson 75116–1,* IFGP) and said this is the first recorded occurrence in the Panamint Range. The nearest previously recorded locality is 187 km northeast at Lake Sabrina, Inyo County, California, according to Dr. Hawksworth.

Juniperus occidentalis has been reported by Griffin and Critchfield (op. cit.) in the Panamint Range north of Panamint Pass. South of the pass I noted only a few large trees on the northeastern slope of Sentinel Peak.

The Sentinel Peak bristlecone pines warrant further study, including additional chemical analysis. One of the distinguishing characteristics used by Bailey (Ann. Missouri Bot. Gard. 57:210–249. 1970) in referring western stands of bristlecone pine to a separate species (*P. longaeva* D. K. Bailey) was the olfactory/chemical difference he noted. Zavarin and Snajberk (Biochem. Systematics 1:39–44. 1973) analyzed the wood turpentines of the eastern and western populations and found that the western stands they sampled had mainly α-pinene as the dominant monoterpene (85.3 to 98.2 percent) and 3-carene less than 2.5 percent. The eastern stands were characterized by 3-carene as the main component (62.7 to 92.1 percent) and α-pinene less than 5.3 percent. Chemical analysis of ten trees from Sentinel Peak by Zavarin (pers. comm., Oct. 1975) places this stand with the eastern populations; α-pinene ranged from 1.6 to 13.7 percent and 3-carene ranged from 76.1 to 90.9 percent. Thus, one important character distinguishing *P. longaeva* is not as clear cut as previously assumed. More detailed studies of the southern desert peak bristlecone pine stands (Telescope and Sentinel Peaks in California, the Spring Mountains, Nevada, and the San Francisco Mountains, Arizona) may reveal further evidence to clarify the taxonomic status of the western stands. Possibly treating the bristlecone pine complex as a single species with the western populations named as a subspecies would be more appropriate.—LeRoy C. Johnson, Pacific Southwest Forest and Range Experiment Station, Forest Service, U. S. Department of Agriculture, Berkeley, California 94701

Charles Wright's "El Paso" Collections and the Type Locality for Psathyrotes scaposa (Compositae).—Type localities for several taxa collected by Wright and first described by A. Gray in *Plantae Wrightianae* (Smithsonian Contr. Knowl. 3(5), 1852, and 5(6), 1853) are given variously as "Stony hills above El Paso", "Along the Rio Grande near El Paso", "Around El Paso", etc. Strother and Pilz (Madroño 23:24–40. 1975) indicated that the type locality for *Psathyrotes scaposa* A. Gray is "probably considerably southeast of El Paso, Texas, but it cannot be determined with certainty", although Gray's protologue (Pl. Wright. II:100.) gives "Stony hills above El Paso". A recent collection vindicates Gray/Wright: New Mexico, Doña Ana Co., Cerro de Los Muleros, west side of Rio Grande, near Mexico boundary, 24 May 1975, *T. K. Todsen 55241,* NMC, TEX, UC. (Note: Correct date for Wright's collection is May 1852, not 1851 as given by Strother and Pilz.)

Comparison of *Plantae Wrightianae* and a transcript of Wright's field notes (prepared and annotated by I. M. Johnston, 1940; original at GH, copy in Biology Library, Univ. California, Berkeley; cf. McKelvey, *Botanical exploration of the trans-Mississippi west, 1790–1850,* 1955, p. 1603 ff.) indicates that Gray frequently combined Wright's separate gatherings and that Gray frequently used "El Paso" not only for collections that Wright originally recorded under "El Paso" (or environs) but also for those recorded as "Frontera" (or environs), including "rocky hills near Frontera" and "rocky ridges across river from Frontera". The name Frontera was associated with T. Frank White's rancho, which was just north of the pass of the Rio Grande on the east side, about 9 km northwest of the plaza in

present El Paso. Wright's "rocky ridges across river from Frontera" may correspond to present Cerro de Los Muleros (across Rio Grande from site of Frontera) and probably is a good approximation to the type of locality for *Psathyrotes scaposa* and, perhaps, other plants treated in *Plantae Wrightianae.*

"El Paso" in Wright's time (1849–1852) corresponds to present Cd. Juarez, Chihuahua. Gray inexplicably cited El Paso as being in southern New Mexico. Wooton (Bull. Torrey Bot. Club 33:561–566. 1906) discussed Wright's itinerary and, perhaps similarly confused, mistakenly indicated that El Paso was then in New Mexico, which he wrongly outlined as "a somewhat indefinite area extending from well down in what is now . . . Chihuahua . . . and including some of western Texas . . .".—THOMAS K. TODSEN, Box 1464, Las Cruces, New Mexico 88001.

REVIEW

Die Vegetation Osteuropas, Nord- und Zentralasiens. By HEINRICH WALTER. xxi+ 452, 363 figs. Gustav Fischer Verlag, Stuttgart. 1974. 149 DM ($66.).

A plant ecologist acquainted with western North American vegetation who travels eastward from Europe may sense an increasing familiarity with the vegetation. Familiar plants occur in familiar associations and habitats. An American can recognize *Artemisia frigida* and *Linaria vulgaris* as he walks across an airport that might be at Jackson, Wyoming, but is actually at Omsk in Siberia, be shocked at what looks like an Eastern Siberian shrub of *Pinus pumila* out of place in the Wind River Mts. but is actually a young, snow-deformed *Pinus albicaulis,* recognize *Hordeum jubatum* as the ubiquitous weed in several Yakutian cities, remember the larch forests of the Bitterroot Mts. as he becomes acquainted with the beautiful eastern Siberian taiga with *Larix dahurica,* recognize in a patch of talus in the Cherski Mts. the same *Dryopteris fragrans* he saw in the same kind of site near Atlin Lake in British Columbia, see *Eurotia* (*Ceratoides*) hundreds of kilometers disjunct both in a steppe island within the boreal taiga at Kluane Lake in the Yukon or along the Lena River. Other boreal and arctic-alpine similarities are exceedingly numerous.

Walter's authoritative book describes this Eurasiatic vegetation. It is ecological and excellent. For those to whom the Cyrillic alphabet is a block, Walter makes readily available a very rich and detailed botanical literature.

The Introduction (21 pp.) describes the flora, methods of studying vegetation, the zonal kinds of vegetation, and Walter's climatic diagrams. Arctic desert and tundra (31 pp.), boreal coniferous forest (53 pp.), transitional mixed coniferous-deciduous forest (25 pp.), nemoral deciduous forest (30 pp.), steppe (68 pp.), semi-desert and desert (99 pp.), and mountain vegetation (Urals, Altai, Crimea, and Caucasus) (82 pp.) are graphically, vividly, perceptively discussed. Walter is a superb ecologist with worldwide field experience, and his treatment is most instructive.

He is an adherent of no one phytosociological method; he uses the results of a great variety of methods of study. He shows the similarity in results achieved when stands of vegetation, which may be points on a continuum of interacting ecological sequences or ecological types, are floristically described in different ways. Since kinds of vegetation are not documented in the book by stand-species matrices, the reader must accept the interpretations suggested, but the literature references are adequate for further search and understanding.

Comparisons with western North American vegetation are often explicit, as for the aspen parkland (p. 158 ff.). No American reader will fail to be stimulated, to question our present answers to our plant ecological questions, to expand his own horizons.

The book closes with a selected reference list and a fine index to plant species and subjects. It is richly illustrated with photographs, habit sketches of particular species. diagrams, and maps. Many maps lack a scale; some lack a latitude-longitude net. Unfortunately the price is out of this world.—JACK MAJOR, Department of Botany, University of California, Davis 95616.

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Editorship of Madroño.—Terms of current editors of Madroño end 31 Dec 1976. The Board of Directors of the California Botanical Society have appointed Barbara D. Webster to serve as Editor and Grady L. Webster to serve as Associate Editor. After 1 Jul 1976, manuscripts intended for publication in Madroño should be sent to Barbara D. Webster, Department of Agronomy and Range Science, University of California, Davis 95616.

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CHROMOSOME NUMBERS FOR EUPHORBIA (EUPHORBIACEAE) FROM WESTERN NORTH AMERICA

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Euphorbia L. has undergone much evolutionary diversification in western North America. Until the study of Urbatsch et al. (1975), practically no information was available on the role played by aneuploid and euploid changes in chromosome number in the evolution of American Euphorbias. Perusal of reports by Hans (1973) and Urbatsch et al. (1975) reveals that many taxa remain cytologically unknown, particularly in the southwestern United States and northern Mexico.

Methods

Immature cyathia were killed and fixed in the field in modified Carnoy's fixative (4–6 chloroform: 3 ethanol: 1 glacial acetic acid, v:v) and were stained for 24 to 48 hours in iron-acetocarmine. Anthers were squashed in Hoyer's solution according to the methods of Beeks (1955). Chromosome counts were determined from meiotic microsporocytes, and camera lucida drawings were prepared to document the reports. Vouchers are at ASU.

Results

Twenty-seven counts representing sixteen taxa were made (Table 1). First reports are presented here for nine species and one variety, and previously unreported chromosome numbers are documented for two additional taxa (figs. 1–15).

Discussion

Considerable aneuploid and euploid variation is present among the taxa sampled in subg. *Chamaesyce*. Hans (1973) suggested that the base number for *Euphorbia* as a whole is $x = 7$, and Urbatsch et al. (1975) indicated a suspected base number of $x = 7$ for subg. *Chamaesyce*. If $x = 7$ is the base number for subg. *Chamaesyce*, then numbers of $n = 6$, 8, and 9 are probably aneuploid changes from that base. This was suggested for *Euphorbia* as a whole by Hans (1973).

Hans (1973) indicated that $n = 13$ is an unusual chromosome number in *Euphorbia*. Presence of this number in several taxa of subg. *Chamaesyce* may represent aneuploid change from a tetraploid number of either $n = 12$ or $n = 14$ or a direct amphidiploid from a hybrid between

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TABLE 1. CHROMOSOME COUNTS FOR TAXA OF EUPHORBIA. [a] = first report for this taxon; [b] = previously unpublished number for this taxon; [c] = some cells with 12 II + 2 I.

Subg. *Agaloma* (Raf.) House

E. plicata S. Wats.[a] Sonora, E of Mazatán, *Lehto 19342, 2n* = 14 II (fig. 1).

Subg. *Chamaesyce* Raf.

E. albomarginata T. & G. Sinaloa, N of Los Mochis, *Lehto 19518, 2n* = 24 II[b] (fig. 2). Arizona, Pima Co., 2 mi W of Robles, *Keil 11152, n* = 18 I/ pole (fig. 3). New Mexico, Socorro Co., 12 mi E of Río Grande on US 60, *Keil 10740, 2n* = ca. 24 II.

E. arizonica Engelm.[a] Arizona, Maricopa Co., White Tank Mts. Regional Park, *Keil 11172, 2n* = 13 II (fig. 4); Pima Co., Organ Pipe Cactus Natl. Mon., *Lehto 19231, 2n* = 13 II.

E. capitellata Engelm.[a] Arizona, Maricopa Co., McDowell Mts. Regional Park, *Lane 1789, 2n* = 13 II[c] (fig. 5).

E. fendleri T. & G. var. *fendleri.* New Mexico, Rio Arriba Co., 14 mi N of Espanola, *Keil 10714, 2n* = 14 II.

E. florida Engelm.[a] Sonora, 8 mi N of Hermosillo, *Lehto 19345a, 2n* = 8 II. Arizona, Pima Co., just W of Quijotoa, *Keil 11003, 2n* = 8 II (fig. 6); 3 mi N of Santa Cruz Co. line on I-19, *Keil 11085A, 2n* = 8 II.

E. hirta L. var. *hirta.* Sinaloa, 18 mi NE of Choix, *Lehto 19553A, n* = 8 I/ pole (fig. 7).

E. hyssopifolia L.[a] Arizona, Santa Cruz Co., 7 mi W of I-19 on Ruby Rd. *Keil 11053, 2n* = 6 II; just off I-19 on Ruby Rd., *Keil 11096, n* = 6 I/ pole (fig. 8).

E. indivisa (Engelm.) Tidestr.[a] Sonora, 10 mi NE of Imuris, *Lehto 19381, 2n* = 9 II (fig. 9).

E. lata Engelm. New Mexico, Socorro Co., 12 mi E of Río Grande on US 60, *Keil 10741, 2n* = 28 II.

E. melanadenia Torr.[a] Arizona, Maricopa Co., McDowell Mts. Regional Park, *Lane 1789, n* = 8 I/ pole (fig. 10).

E. pediculifera Engelm.[a] Sonora, 21 mi W of Sonoita, *Lehto 19237, 2n* = 12 II + 1 I (fig. 12). Arizona, Santa Cruz Co., Pena Blanca Lake, *Keil 11010, 2n* = 12 II (fig. 11); 5.5 mi W of I-19 on Ruby Rd, *Keil 11039, 2n* = 13 II + 1 I (fig. 13).

E. polycarpa Benth. var. *hirtella* Boiss. Sonora, 8 mi N of Hermosillo, *Lehto 19358, 2n* = 13 II.

E. polycarpa Benth. var. *polycarpa*[a]. Arizona, Maricopa Co., McDowell Mts. Regional Park, *Lane 1790, n* = 13 I/ pole (fig. 14).

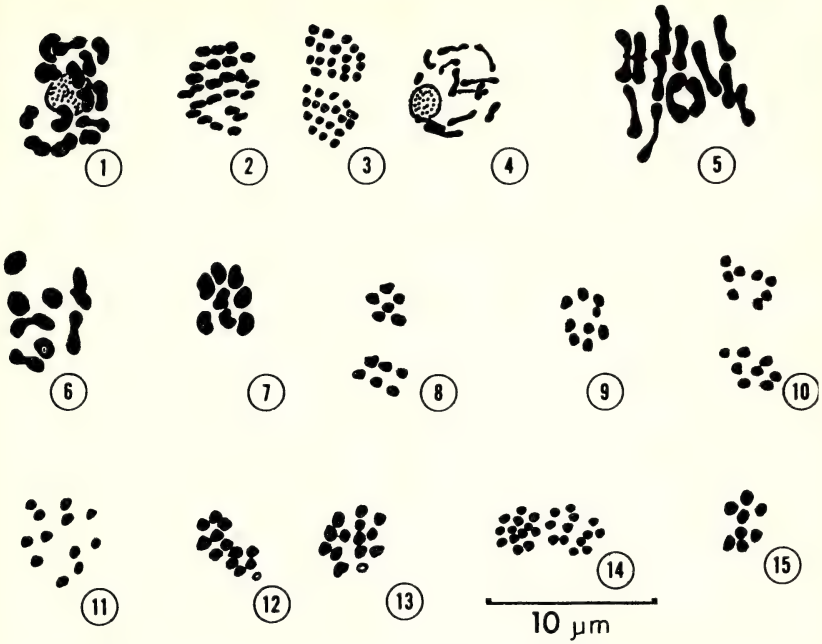
E. setiloba Engelm.[a] Sonora, 20 mi E of Altar, *Lehto 19282, 2n* = 8 II (fig. 15); 8 mi N of Hermosillo, *Lehto 19359, 2n* = 8 II. Arizona, Maricopa Co., McDowell Mts. Regional Park, *Lane 1788, 2n* = 8 II.

Subg. *Poinsettia* (Graham) House

E. eriantha Benth. Sonora, 8 mi N of Hermosillo, *Lehto 19357, 2n* = 14 II. Arizona, Maricopa Co., White Tank Mts. Regional Park, *Keil 11177, 2n* = 14 II.

$n = 6$ and $n = 7$ parent taxa. An aneuploid origin for $n = 13$ plants is favored by my reports of $2n = 12$ II, $2n = 12$ II + 1 I, and $2n = 13$ II + 1 I for *E. pediculifera.*

Euphorbia albomarginata was reported by Urbatsch et al. (1975) to have $n = 12$. My reports of $n = 18$ and $n = 24$ for this taxon indicate that it comprises several polyploid races with a base of $x = 6$. Further investigation should be undertaken to determine whether the different



FIGS. 1–15. Camera lucida drawings of *Euphorbia* chromosomes. See Table 1 for interpretation and voucher citation. 1. *E. plicata,* diakinesis. 2. *E. albomarginata,* metaphase I. 3. *E. albomarginata,* anaphase I. 4. *E. arizonica,* diakinesis. 5. *E. capitellata,* metaphase I (superimposed chromosomes moved for clarity). 6. *E. florida,* diakinesis. 7. *E. hirta* var. *hirta,* metaphase II (only one half of cell shown). 8. *E. hyssopifolia,* metaphase II. 9. *E. indivisa,* metaphase I. 10. *E. melanadenia,* anaphase I. 11. *E. pediculifera,* metaphase I. 12. *E. pediculifera,* metaphase I. 13. *E. pediculifera,* metaphase I. 14. *E. polycarpa,* anaphase I. 15. *E. setiloba,* metaphase I.

cytotypes represent morphologically or geographically distinguishable races. Populations of *E. albomarginata* should be checked to determine whether there are any extant diploids.

Euphorbia arizonica and *E. setiloba* are similar in many respects and were considered by Wheeler (1941) to be closely related. My chromosome counts for these taxa, $n = 13$ and $n = 8$ respectively, indicate a considerable cytological hiatus between the two. This gap is similar to that reported by Johnston and Turner (1962) and Strother (1969) for closely related plants in *Dyssodia* (Compositae), also $n = 8$ and $n = 13$. A satisfactory explanation for such a gap is not yet available in either case.

My report of $n = 8$ for *E. hirta* var. *hirta* differs from previous reports for this species. Hans (1973) summarized reports for *E. hirta* published by Indian workers ($n = 9$, $2n = 20$, $2n = 12$). The name, *Euphorbia hirta,* has been misapplied in some cases to plants now known correctly

as *E. pilulifera* L. (Wheeler, 1941). Since *E. hirta* is a very widespread taxon and has become established as a weed in many regions, it is not unreasonable to suspect that it may have undergone localized aneuploidy. Before such an explanation is accepted, however, identity of plants from which previous reports were made needs to be checked. If the various reports do, indeed, all apply to the same taxon as currently recognized, the systematics and evolution within this group would make an interesting topic for future work.

The great variety of chromosome numbers in *Euphorbia* subg. *Chamaesyce* in North America is indicative of the very significant role that chromosomal changes have had in the evolution of these taxa. More reports from additional taxa and from additional populations will be needed before evolutionary relationships in subg. *Chamaesyce* can be satisfactorily elucidated.

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GROWTH FORMS OF LARREA TRIDENTATA

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The population dynamics of *Larrea tridentata* have been of considerable concern to plant ecologists. Interest has centered around questions of geographical distribution (Shreve, 1942; Gardner, 1951; Yang, 1953; Rickard and Murdock, 1963; Beatley, 1974), spacing of individuals (Barbour, 1969a; Woodell et al., 1969; Wright, 1970), seed germination and seedling establishment (Knipe and Herbel, 1966; Barbour 1968; Sheps, 1973), and growth patterns (Spalding, 1904; Runyon,

1934; Wright, 1970; Vasek and Barbour, in press). Growth patterns of *Larrea* shrubs and response to environmental stresses have been described in developmental terms by Runyon (1934), Johnson et al. (1975), Wright (1970), and Vasek and Barbour (in press). In the Mojave Desert, circles of *Larrea* shrubs surrounding "bare" areas have been observed by Vasek et al. (1975), who interpreted these formations as clonal rings. Different developmental stages were noted from single-stemmed seedlings and large clumps to rings of satellite clumps. Clonal rings usually occur on mounds raised a few decimeters or so above general terrain level. Similar mounds were observed in Arizona by Wright (1970) who suggested several possible modes of origin.

Two questions about creosote rings immediately arise: (1) are they in fact clonal? and (2) what is their longevity? If they persist for extreme periods and undergo fragmentation, the definition of an individual *Larrea* shrub becomes problematical (Vasek and Barbour, in press). The purpose of this paper is to test whether rings are indeed clonal and to assess probable longevity. Members of a clonal ring by definition should be genetically identical whereas seedlings should be genetically diverse. Isoenzyme analysis provides a convenient test for genetic identity (Brewer and Sing, 1970).

Material and Methods

Study Sites

Observation and samples of rings were made at Lucerne Valley and Johnson Valley, San Bernardino County, California. Those two sites are located north of the San Bernardino Mountains and south of the Fry Mountains and Ord Mountains. The Lucerne Valley site has a sandy soil and may receive considerable drainage water from the San Bernardino Mountains. The Johnson Valley site has a rockier soil than Lucerne Valley and its elevated topography in a basin removed from the San Bernardino Mountains precludes drainage input. Thus, vegetation in the Johnson Valley site seems to be under more xeric conditions than that in the Lucerne Valley. The predominant plant community occurring in the two sites is a creosote bush scrub community with *Larrea tridentata* and *Ambrosia dumosa* (nomenclature follows Munz, 1974) occurring as dominants. A few additional observations and samples of some creosote rings were made in Death Valley (Inyo County, California) and Indio Hills (Riverside County, California).

Field Methods

Eight rings and 20 seedlings were sampled in Lucerne Valley and Johnson Valley. Leaf samples from a ring were collected from satellite shrubs at subjectively chosen points around the ring. Voucher specimens were not collected; however, the sampled creosote rings were marked and are available for further verification. Samples of seedlings were taken at the Lucerne Valley site in a 20 m^2 plot from young shrubs that had not yet

developed a root crown, thus the possibility of sampling two individuals from a clone was avoided. Leaf samples were placed in plastic bags immersed in ice and taken to the laboratory for isoenzyme assay. Isoenzyme assay was performed approximately 24 hours after collection of samples. The average radius of rings in Lucerne Valley and Johnson Valley was measured. Other putative clones were sampled for isoenzyme assays: one in Death Valley and two in Indio Hills.

Laboratory Analysis

Two enzyme systems from leaf extract were used in this study: peroxidase and acid phosphatase. Leaf material was washed with 95 percent ethanol and rinsed with water. Washed leaf material was ground with an equal weight (1.25 g) of sand and 3 ml of acetate buffer (pH 5.4; 0.1 M) into a homogeneous paste. This paste was centrifuged for 20 minutes at 10,000 r.p.m. The supernatant was saved and the pellet discarded. A 12 percent sucrose solution was made with the supernatant, and 15 μl of this solution were used for electrophoresis. Electrophoresis was done in 7.5 percent acrylamide gel (pH 8.9) for 3 hours with a tris glycine buffer (pH 8.3). The staining procedure for the peroxidase and acid phosphatase isoenzymes followed Brewer and Sing (1970) and Burstone (1962) respectively.

Results

The probable development of creosote rings can be observed in the field. A continuous series of stages occurs from single stemmed seedlings to large clumps with dead branches in the center to circles of satellite clumps. A continuous ring is probably an intermediate stage in this developmental sequence. An overhead view of a continuous ring shows a sterile center, the canopy, and the exterior of the ring (see photo in Vasek and Barbour, in press). A continuous ring occurs on a mound of sand at a slightly higher elevation than the surrounding soil surface. The mound has a loose sandy surface layer while the intermound soil has a more gravelly surface. Tunnels produced by animal activity are often found in the sandy mound both in the central area and in the periphery of the ring. In the outer edge of the sand mound, a mass of both living and dead root crowns is present. Root growth occurs predominantly outward, away from the center of the ring. Roots vary in length up to and sometimes longer than 3 m. Occasionally dead pieces of root crown are found in the sterile center of small rings. Using radio carbon techniques, growth rates for rings have been estimated under the assumptions that a ring is clonal and that dead root crown in the sterile center represents original material from the clone. Two rates were derived reflecting different ring growth rates under different environmental conditions. On a south-facing rocky slope, the growth rate was about 0.26 mm of radius per year (Vasek et al., 1975) and on a sandy substrate with relatively more mesic conditions, the growth rate was about 1.43 mm of radius per year (Vasek and Johnson, unpublished data).

Different types of creosote rings found in Johnson Valley and Lucerne Valley are shown in Figure 1. Fragmented rings may consist of only one large fragment giving them a "horseshoe" shape (fig. 1 B) or they might have many fragments (fig. 1 C). Secondary rings (sub-rings) growing from a primary ring are also shown in Figure 1. The primary ring can be either continuous (fig. 1 D) or fragmented (fig. 1 E). Other types of rings observed in the field are permutations of growth forms shown in Figure 1.

A total of 15 isoenzymes was found for the peroxidase system and six isoenzymes were noted in the acid phosphatase system. Representative zymograms of the peroxidase and acid phosphatase isoenzymes found in this study are shown in Figure 2. Figures 3 and 4 show zymograms of assays done for ten seedlings and for a creosote ring respectively. Each vertical row of bands represents an individual genotype with respect to the particular system used.

Discussion and Conclusions

Based on seedling samples, the probability of two individuals having the same genotype for peroxidase is 0.15 and that for acid phosphatase is 0.30. If the genetics of these two systems are independent of each other, then the probability of two seedling individuals having identical genotypes for both systems is 0.045. A survey of 20 seedling samples indicated that no individuals had identical isoenzymes for both peroxidase and acid phosphatase systems. This survey therefore provides evidence supporting the basic assumption that any two seed-derived individuals will probably differ in at least one isoenzyme system. *Larrea* is probably self-compatible (Hunziker et al., 1972), and thus could produce electrophoretically identical progeny by self-pollination. However, this is unlikely since genetic homogeneity was not seen in the seedling samples. In addition, a high degree of homozygosity would be required for a self-compatible plant to produce electrophoretically identical progenies. By negation of the proposed assumption, if two individuals contain identical isoenzymes for both systems they probably were not derived from different seeds; therefore they are clonal.

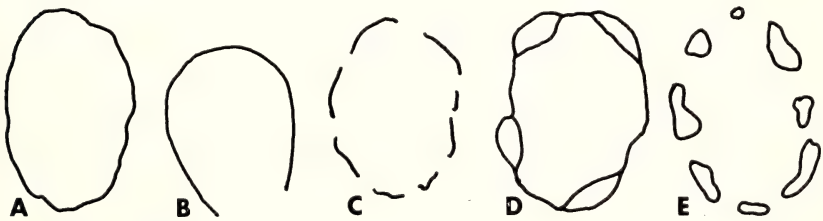

Fig. 1. Types of creosote rings found in Johnson Valley and Lucerne Valley. A=continuous creosote ring, B=creosote ring with one fragment only, C=ring with many fragments, D=secondary rings growing from a continuous primary ring, E=secondary rings growing from a fragmented primary ring.

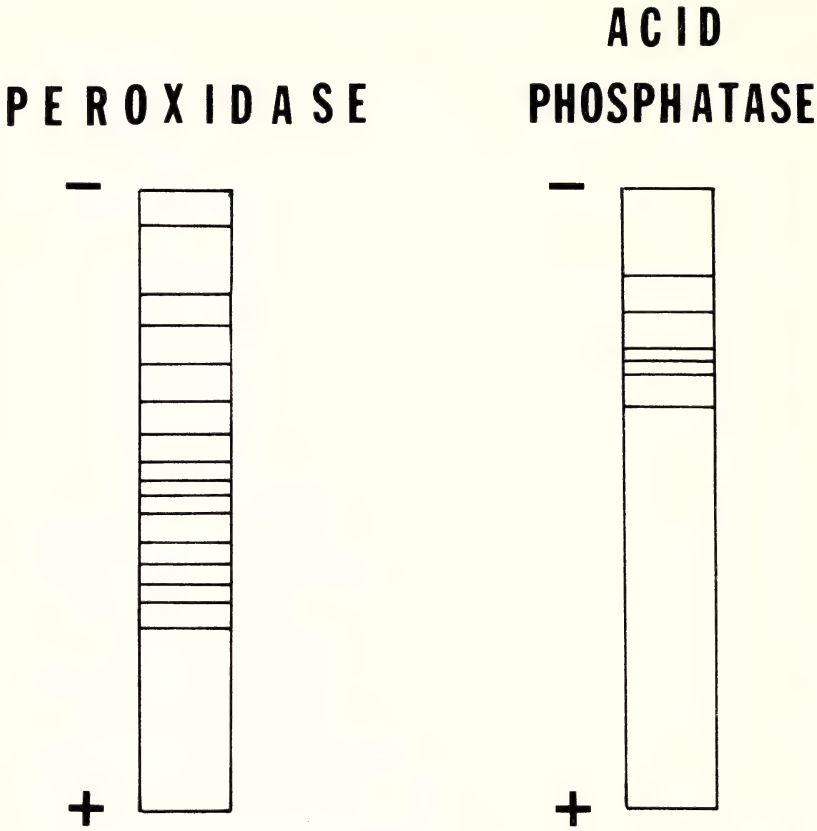

FIG. 2. Representative zymograms showing the locations of all isoenzymes found in the peroxidase and acid phosphatase systems.

The zymogram of assays done for a creosote ring (fig. 4) indicates that samples from the ring have identical isoenzymes for both systems; hence this particular ring is probably clonal. The analysis of other putative clones is given in Table 1. A few sample sets were assayed only for the peroxidase system. The probability of four or more individual seedlings having identical genotypes for the peroxidase system is very small. Thus, these sample sets are probably clonal (sample sets 2, 5, and 7) or partly clonal (sample set 10). The clonal process in Avra Valley, Arizona, has been described as either root sprouting, stem layering, or crown splitting (Wright, 1970). In the sites studied here, only crown enlargement and fragmentation were observed as clonal processes.

The choice of hypothetical clones (Table 1) was based on aerial photographs and ground level inspections. Aerial photographs were not always sufficient to determine whether growth forms were clonal. From an aerial photograph the clumps in sample set 1 (Table 1) appeared to be

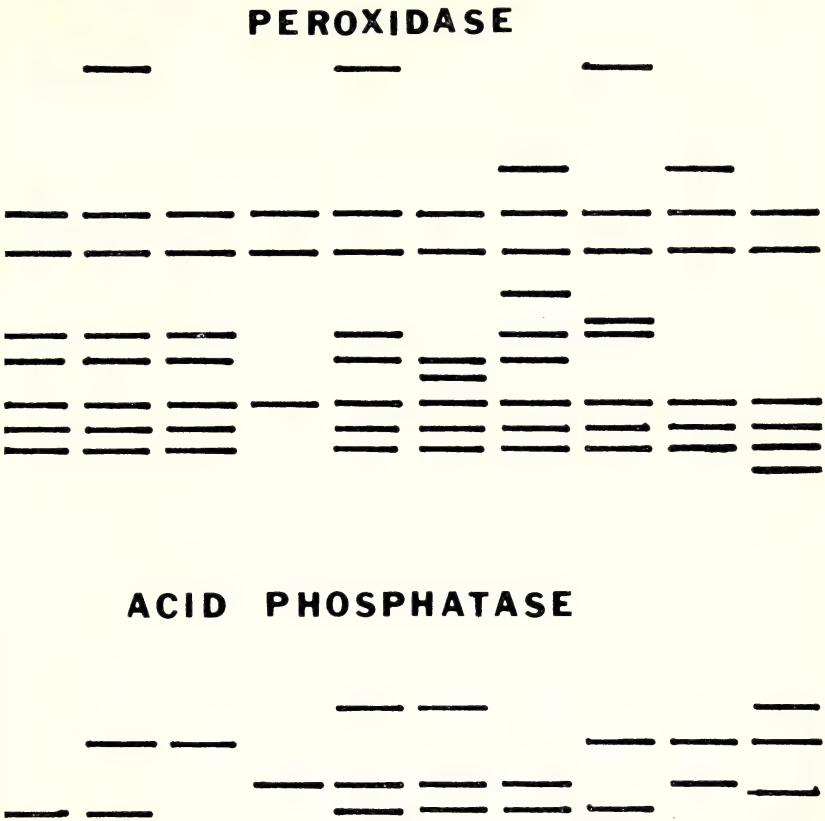

FIG. 3. Zymogram of 10 seedling samples for the peroxidase and acid phosphatase system.

in a circular pattern, but ground level inspection of clump arrangement indicated the pattern was not circular and thus these clumps probably did not have a common clonal origin. Isoenzyme analysis showed that these clumps had different genotypes, which confirms ground level interpretation of growth forms. A variety of clonal growth forms was tested as shown in Table 1. All continuous rings were clonal; however, fragmented rings were either clonal or showed a mixture of clonal and seedling material. Mixture of seedling and clonal material probably represents the germination of seeds and establishment of seedlings in the vicinity of an established shrub. Wright (1970) suggests that the microenvironmental conditions in the vicinity of an established shrub might favor the germination of seeds in its vicinity.

All sites studied here had a more or less sandy substrate; hence the growth rate of 1.43 mm of radius per year is more representative of the growth rates of rings measured in Lucerne Valley and Johnson Valley. The results are shown in Table 1. In Johnson Valley, age approximations

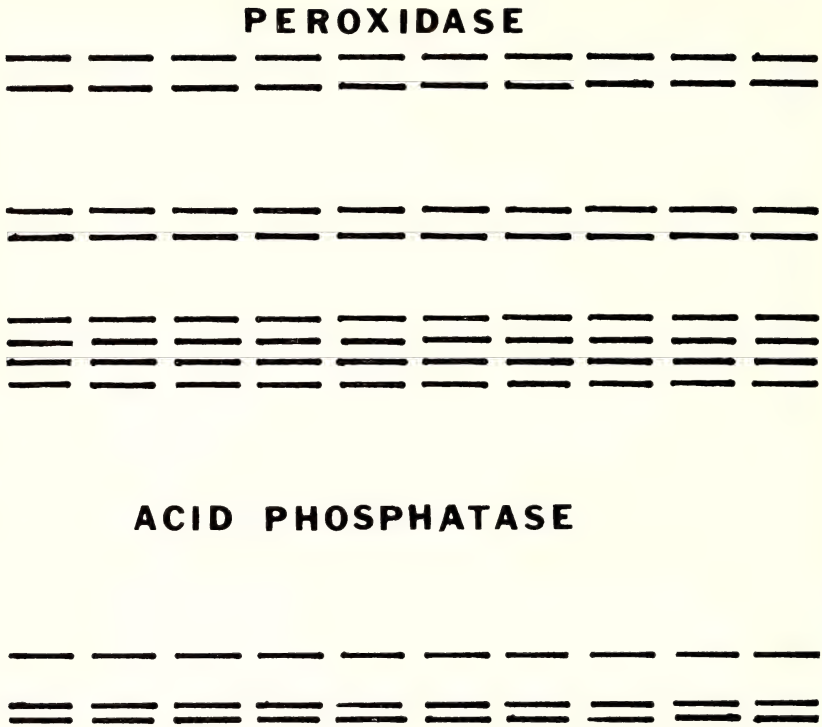

FIG. 4. Zymogram of 10 samples from a creosote ring for peroxidase and phosphatase system.

are probably a minimum estimate of age, since the environment is relatively more xeric than that in Lucerne Valley.

Several stages in the development of a creosote ring are documented in Table 1. Sample set 2 was a large clonal clump. Senescence in the center of a clump produces a clonal ring (sample set 3). Fragmentation of a clonal ring is the probable cause in the formation of a ring of satellite clumps (sample sets 7 and 8). Establishment of new genetic material in a creosote ring might occur at a later stage in the life history of a creosote ring (sample sets 9, 10, and 11). At any stage in this developmental sequence, there is variation in the average radius of rings and consequently in the approximate age of rings. Thus, sample set 8 is older than sample set 3 in developmental terms but younger in approximate chronological age. The observed disparity between developmental and chronological ages indicates that the shaping of these developmental forms is dependent on factors other than the radial growth.

The clonal abilities of *Larrea* may be relevant to several aspects of population dynamics. Sheps (1973) indicated in a study of seed germination in *Larrea* that survival of *Larrea* in nature might involve factors

Table 1. Characteristics of Growth Forms of Creosote Bush. Growth forms A through E are shown in Figure 1. *Sample could not be visualized as being a ring of satellite clumps from ground level. **Leaf sample was assayed for peroxidase system only. ***Radius not measured. †Age estimated with growth rate of 1.43 mm of radius per year.

Sample set	Type of growth form	Number of samples	Number of fragments	Average radius in m	Number of genotypes	Location	Estimated age in years†
1	*	10	10	—	10	Johnson V.	—
2	Clump	4	—	—	1**	Death V.	—
3	A	10	—	4.4	1	Johnson V.	3077
4	D	12	—	7.8	1	Johnson V.	5454
5	D	6	—	1.7	1**	Johnson V.	1189
6	B	8	1	2	1	Lucerne V.	1399
7	C	4	2	—	1**	Indio	***
8	C	4	3	1.5	1	Johnson V.	1049
9	B	2	1	2.5	2	Lucerne V.	—
10	C	8	2	—	2**	Indio	—
11	E	8	5	3.6	2	Lucerne V.	—

other than seed germination. The clonal abilities of *Larrea* might be one important factor contributing to the survival of *Larrea* in nature. Cloning in *Larrea* allows the perpetuation of a population to be independent of the hazardous process of seed germination (Muller, 1951). Age estimations of clonal rings indicated that the vegetative persistence of *Larrea* is enormous. The longevity of *Larrea* clones, as in all long-lived clones, might preserve a population in which an advantageous mutation has arisen (Muller, 1951). The survival of three chromosomal populations in *Larrea* (Barbour, 1969b) could have been favored by this longevity. Another aspect related to the clonal abilities of *Larrea* is the distribution of individuals in a population. Since cloning obscures any precise identification of an individual, an arbitrary definition of an individual by different authors could have contributed to contradictory results in pattern studies of *Larrea* (King and Woodell, 1973; Barbour, 1973; Anderson, 1971).

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REGENERATION OF INTRODUCED SPECIES OF CISTUS (CISTACEAE) AFTER FIRE IN SOUTHERN CALIFORNIA

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Establishment of vegetative cover for erosion control on barren or disturbed wildland sites is an important aspect of watershed management in Southern California. Disturbances resulting from construction activities pose a particularly serious problem. Early attempts to extend the cover provided by native chaparral shrubs onto these sites by direct seeding and transplants were of only limited success (Juhren, 1956). A number of introduced shrubs from areas of similar Mediterranean climate were subsequently tested to find species that might perform more satisfactorily in low-maintenance plantings (Juhren, 1956; Hellmers and Ashby, 1958; Ching, 1959).

Among the most promising introductions were species of *Cistus* (rockrose) native to the Mediterranean Basin (Juhren, 1956). These

deep-rooted, evergreen shrubs occur widely as components of the Mediterranean macchia (maquís) and garrigue plant associations (Knapp, 1962; Le Houerou, 1974), which are analogous to the California chaparral and coastal sage scrub (Naveh, 1967; Zinke, 1973). The results of several studies (Martin and Juhren, 1954; Laure et al., 1961; Ching and Stewart, 1962; Montgomery and Cheo, 1969) have indicated that individual plants and stands of *Cistus* may be less flammable than most dominant chaparral shrubs. Thus in addition to providing cover, wildland plantings were thought to have potential in reducing the incidence of brush fires along mountain roads, near homes, and around campgrounds (Martin and Juhren, 1954; Stewart, 1961).

Despite the interest in *Cistus* for erosion control and fire hazard reduction, little attention has been given to the ecology and ultimate fate of these plants in Southern California. Knowledge of their response to fire is of particular interest. Recurring fires are a natural and inevitable part of the chaparral environment (Cooper, 1922; Hanes, 1971). Given enough time, fire would eliminate plantings of *Cistus* or any other shrub unless the species possesses adaptations to enable it to survive and recover after burning. Stands of *Cistus* destroyed by fire in the Mediterranean Basin regenerate very rapidly, and the species are well adapted to frequent burning (Knapp, 1962). Naveh (1974) found that *C. villosus* and *C. salvifolius* in Israel are facultative resprouters; they regenerate after fire by new growth from dormant buds in the root crown of the burned plants as well as from seed. It has also been shown that *Cistus* seed germination increases after fire (Naveh and Dan, 1973). *Cistus* species are classified as active pyrophytes and are often encountered as pure stands in areas of the Mediterranean Basin where the frequency of fire is particularly high (Le Houerou, 1974).

The first observations of the response of *Cistus* to fire in Southern California were reported by Martin and Juhren (1954). Following burning tests of several species grown under garden conditions, large numbers of seedlings appeared around the base of burned plants. Relatively few seedlings were found beneath unburned controls. In addition, many of the burned shrubs resprouted from the root crown (Martin and Juhren, 1954). These observations substantiate the "fire-type" nature of *Cistus,* but they do not answer the question of whether wildland stands can become reestablished spontaneously after fire. Of critical importance in this regard is the ability of the plants (seedlings and/or resprouts) to compete successfully with native species during the early stages of post-fire succession.

A major wildfire in 1968 partially destroyed one of the *Cistus* field plantings and provided an opportunity to investigate further the fire ecology of *Cistus* in Southern California. Presented in this paper are the results of analysis of the burned and adjacent unburned areas carried out four years after the fire.

Study Area

The *Cistus* field planting involved in fire is located at Dillon Divide on the coastal exposure of the San Gabriel Mountains approximately 10 km northwest of the city of Sunland, California, at 820 m (2700 ft) on a 30–35° north-facing slope. The general climate of the area is Mediterranean defined by a relatively short winter of cool temperatures and occasional heavy rain storms alternating with a long, hot dry season. Mean annual precipitation at the site extrapolated from isohyetal maps (Los Angeles County Flood Control District, 1975) is 50 to 60 cm. Soils were classified as Entic Haploxerolls (USDA Soil Conservation Service, 1973). They are granitic in origin (pH 6.0 to 6.5) with a dark grayish brown A-horizon of loamy-sand texture overlying a pale brown C-horizon of highly weathered parent rock. Depth varies from less than 50 cm near the top of the slope to 150 cm or more at the base of the slope.

The site was cleared as part of the Kagel-Mendenhall Fuelbreak in the mid-1950's (unpublished maps and field reports, Angeles National Forest). Regrowth of native chaparral shrubs from crown sprouts and seedlings was controlled with herbicides. The site originally supported a dense stand of mixed chaparral dominated by *Adenostoma fasciculatum, Quercus dumosa,* and *Ceanothus crassifolius.*

The *Cistus* planting was established in June 1961 (unpublished field reports, LASCA). The Reese fire of the preceding year had burned off the plant cover leaving only charred stumps of the larger shrubs. A total of 1,000 nursery-grown seedlings of *C. villosus* and *C. ladaniferus* in tar paper tubes were set out over an area of 0.4 ha. The plants were irrigated at the time of planting. They received no supplemental water or care thereafter. Initial mortality was high, but by 1964 the population had stabilized at 150 plants (90 and 60 individuals of *C. villosus* and *C. ladaniferus,* respectively). Volunteer seedlings of *Cistus* were not observed in early inspections, although both species had flowered heavily and produced seed. Further observations in the mid-1960's revealed that *Bromus rubens* and several other naturalized annual weeds dominated large areas of the site and that the native shrub cover was becoming reestablished only to a limited degree (unpublished field reports, LASCA).

In September of 1968 the upper third of the *Cistus* stand burned in the large Limerock Canyon fire. The lower part of the planting and an adjacent strip of mature chaparral were left as an island of vegetation within the burned area. The fire appears to have died out as it moved downhill through the open shrub cover and herbaceous vegetation on the old fuelbreak. The leading edge of the fire produced a fairly distinct line extending across the face of the slope and down the western edge of the *Cistus* stand.

The present analysis of the site was undertaken in 1972. At that time the fire line was reconstructed as precisely as possible and marked with

stakes. This line served to divide the site into burned and unburned (control) sub-plots.

Methods

The study area was mapped using a method modified from Cain and Castro (1959). A Brunton compass was positioned along the western edge of the plot, and the area was partitioned into 10° "pie-slice" segments radiating outward for a distance of 30 to 60 m. Direct counts were made of all living *Cistus* plants beyond the cotyledon stage (i.e., larger than 5 cm high) that occurred within each segment. The position of these plants was then determined as the distance from the origin and from the two subtending radii. Care was taken to distinguish between volunteer seedlings and plants developing from root suckers, crown sprouts, or stem layers. Dead *Cistus* shrubs on the burn, where they could be identified, also were mapped. The height of each plant and area of the canopy (derived from paired measurements of width taken perpendicularly) were recorded. From these data estimates of volume were calculated, and the plants were grouped according to the following size classes: A, equal to or greater than 1.00 m^3; B, 0.10 to 0.99 m^3; C, 0.01 to 0.09 m^3; and D, less than 0.01 m^3.

Perennial vegetation on the site was sampled using line interception (Bauer, 1943; Hanes, 1971; Vogl and Schorr, 1972). Five parallel lines 100 m long were placed at 5 m intervals across the face of the slope in approximately a north-south direction from the bottom to the top of the slope. The point at which the intercepts crossed the fire line was recorded. Of the total length, 190.4 m (38.1%) was in the burned sub-plot and 309.6 m (61.9%) in the unburned sub-plot. Data for the large, woody shrubs were analyzed by species. Data for perennial herbs and small sub-shrubs were consolidated into a single group.

Annual grasses and forbs were sampled systematically in May 1973 by placing 1 m^2 quadrats at 10 m intervals along two of the intercept lines. In all, 22 quadrats were set out, nine located in the burned area and 13 in the unburned area. Within the quadrats, the number of individuals of each annual species was counted, and visual estimates of cover were made.

Voucher specimens of all species encountered in the line intercept and quadrat analyses are on file at LASCA. Nomenclature for native and naturalized species is according to Munz (1959); nomenclature for *Cistus* is after Dansereau (1939).

Results

Direct counts of the *Cistus* plants at Dillon Divide grouped by size class are presented in Table 1. The location of each plant is illustrated in Figure 1 with size of the circles being proportional to the size classes. These size classes, when interpreted as age (Daubenmire, 1968), provide a general picture of the structure of the *Cistus* population in the

Table 1. Direct Counts of Cistus Plants at the Dillon Divide Study Site according to Age-size Class. Class A consists largely of old bushes from the original planting. Classes B through D include volunteer plants of decreasing age.

Sub-plot	Number of plants (% of total population)			
	class A ($1.00m^3+$)	class B ($0.10–0.99m^3$)	class C ($0.01–0.09m^3$)	class D ($<0.01m^3$)
Burned				
C. ladaniferus	0	0	39 (31.7)	84 (68.3)
C. villosus	0	14 (11.0)	40 (31.5)	73 (57.5)
Unburned				
C. ladaniferus	49 (77.8)	4 (6.3)	9 (14.3)	1 (1.6)
C. villosus	50 (61.0)	25 (30.5)	2 (2.4)	5 (6.1)

burned and unburned areas. Class A included the remaining original plants set out in 1961 and possibly a few volunteers 8 to 10 years old from seed. Class B included volunteer plants of intermediate age (mostly 4 to 8 years old). Class C was made up of young plants ranging in age from 2 to 4 years. Class D included seedlings 2 years old or less.

A total of 250 volunteer plants of *C. ladaniferus* and *C. villosus* from 1 to 4 years of age were recorded in the burned area (Table 1). The plants showed a distinct clumping pattern around charred stumps of parent shrubs (fig. 1). None of the burned *Cistus* bushes had resprouted from the root crown. In the unburned area, few *Cistus* plants less than 4 years old were found and, where they did occur, they tended to be restricted to openings in the shrub canopy.

Total perennial cover (Table 2) was much lower in the burned area (38.6%) than in the unburned area (72.1%). The burned area was dominated by *Eriogonum fasciculatum* and short-lived perennial herbs and sub-shrubs including *Eriophyllum confertiflorum, Dicentra chrysantha, Antirrhinum nuttallianum* (a biennial), *Lotus scoparius, Haplopappus squarrosus,* and *Helianthemum scoparium* var. *vulgare*. Several of these species are characteristic of the early stages of chaparral succession after fire (Hanes, 1971). Large, woody chaparral shrubs were poorly represented in the post-fire vegetation. Very few seedlings of these species were found. Scattered individuals of *Adenostoma fasciculatum* and *Quercus dumosa* had resprouted from the basal lignotuber (burl); *Eriodictyon crassifolium* was resprouting from rhizomes.

Perennial vegetation in the unburned area was predominately a mixture of *Cistus* and native chaparral shrubs (Table 2). The two species of *Cistus* accounted for over 30 percent of the relative cover. *Eriogonum fasciculatum* was quite abundant, but in many places it was becoming overtopped by *Ceanothus crassifolius. Rhus diversiloba* and *Eriodictyon crassifolium* accounted for most of the remaining cover. Perennial herbs and sub-shrubs were less abundant than in the burned area, but *Eriophyllum confertiflorum* and *Lotus scoparius* occurred extensively in openings between the dominant shrubs.

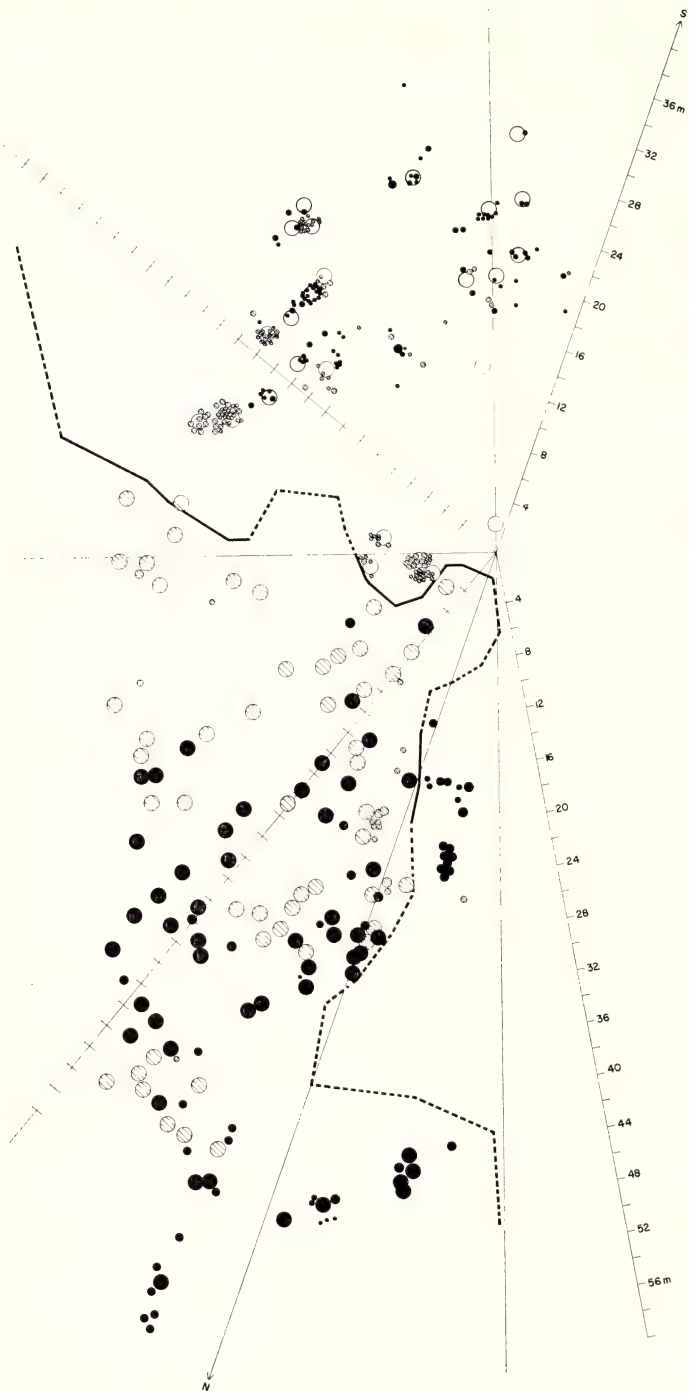

FIG. 1. Map of the *Cistus* stand showing the distribution and age-size class of individuals of both species within the unburned (north) and burned (south) portions of the planting. Size of the circles is proportional to the age-size classes. The fire line is represented by a heavy, solid line where it could be precisely reconstructed and by a heavy, broken line where it was less distinct. The solid black circles indicate *C. villosus*, and circles marked with diagonal lines indicate *C. ladaniferus*. Open circles in the burned area represent the stumps of dead *Cistus* bushes.

TABLE 2. CANOPY COVERAGE AND IMPORTANCE VALUES FOR PERENNIAL PLANTS AT THE DILLON DIVIDE SITE BASED ON LINE INTERSECT ANALYSIS. Total cover is the sum of data for the individual species and species group. Importance values were obtained by adding relative cover, relative density, and relative frequency. The sum of importance values for all species in each sub-plot equals 300 (differences between the data presented and 300 are accounted for by including perennial herbs and sub-shrubs).

Species	Burned area		Unburned area	
	Percent cover	Importance value	Percent cover	Importance value
Eriogonum fasciculatum	13.71	89.70	13.82	53.62
Adenostoma fasciculatum	4.04	18.26	1.07	3.51
Eriodictyon crassifolium	2.63	22.25	13.70	60.28
Cistus villosus	2.26	17.27	6.94	25.35
Cistus ladaniferus	0.53	8.77	13.57	39.72
Salvia mellifera	0.32	3.62	0.00	0.00
Quercus dumosa	0.26	5.27	3.00	14.93
Ceanothus crassifolius	0.05	1.52	3.97	12.80
Rhus diversiloba	0.00	0.00	7.20	30.06
Ceanothus leucodermis	0.00	0.00	0.58	1.67
Others (perennial herbs and sub-shrubs)	14.81	—	8.24	—
Total	38.61		72.09	

Importance values (Curtis and McIntosh, 1951) for each shrub species were calculated from the line intercept data as the sum of relative cover, relative frequency, and relative density (Table 2). By far the most important shrub on the burn was *Eriogonum fasciculatum*. Several plants in the unburned area, including both species of *Cistus*, were of about equal importance.

Annual plant cover consisted largely of naturalized Mediterranean grasses. The dominant species was *Bromus rubens* with average covers of 18.1 and 4.3 percent in the burned and unburned areas, respectively. This species accounted for 83.0 percent of the total annual vegetation in the burned area and 63.2 percent in the unburned area. *Avena fatua* also was abundant in the burned area (2.7% cover). Several other naturalized annuals were encountered in the quadrat analysis but did not contribute to the cover. The native, *Plagiobothrys californicus* var. *fulvescens*, was found in moderate abundance (0.3% cover in the burned area and 0.9% in the unburned area).

DISCUSSION

The present study indicates that it is possible for wildland stands of *Cistus*—at least under certain conditions—to become reestablished and naturalize after fire in Southern California. Regeneration of *C. landaniferus* and *C. villosus* at the Dillon Divide site has been entirely by means of seedlings. Neither species demonstrated the ability to resprout

from the root crown. This observation appears to be inconsistent with reports that *Cistus* species are adapted as resprouters (Martin and Juhren, 1954; Knapp, 1962; Naveh, 1974). However, Naveh emphasized that root crown regeneration in facultative resprouters such as *Cistus* varies greatly from fire to fire according to the age, vitality, and successional status of the plants.

At the time of our analysis, the post-fire *Cistus* stand was composed of volunteer plants ranging in age from 1 to 4 years. Most of the plants appearing in the first and second years after fire must have come from seed produced by the *Cistus* bushes present in the pre-fire stand. Since *Cistus* begins to flower and set seed in two years, these initial seedlings would have provided a seed source to account for more recent germinations. The *Cistus* population is distinctly segregated by species into clumps of plants that are located around the base of the burned parent shrubs. There has been very little spread of the stand into areas not previously occupied by *Cistus*. These observations suggest to us that neither species is aggressive enough to naturalize after fire at the expense of native plants or to become a dominant component in the post-fire succession of chaparral. Mortality within the clumps will probably be high in the next few years, the result being to thin the population to a relatively small number of individuals.

There are certain similarities between our observations and the typical pattern of *Cistus* seed reproduction after fire in the Mediterranean Basin. Naveh (1974) reported that *Cistus* species in the maquís and garrigue vegetation of Israel exhibit a post-fire population explosion that is followed by a drastic reduction in seedling densities probably due to moisture stress and competition. Although germination is quite variable, populations of volunteer seedlings numbering 100 or more plants/m^2 are often found around the base of burned parent shrubs. The greatest increase in germination occurs in the first winter after fire, but seedlings may continue to appear in the second year in microhabitats not occupied by other perennials or by annual invaders (Naveh, 1974).

Two effects of fire are implicated in the regeneration of *Cistus* at Dillon Divide. First, the fire may have directly improved seed germinability. Le Houerou (1974) pointed out that seed germination in *Cistus* is stimulated by fire but added that the effect of burning on the physiology of the seed is not well understood. Unpublished experiments carried out by the first author show that germination in *C. villosus* and, to a lesser extent, *C. ladaniferus* increases substantially following scarification by heating. The second effect involves changes in the site produced by fire, which may have created a more favorable habitat for *Cistus* germination and seedling establishment. Disturbance by fire removed the vegetative cover, thereby increasing the amount of light reaching the ground and reducing competition with shrubs and herbs for soil moisture. Other changes such as the removal of litter, increase in soil fertility, and destruction of phytotoxins as discussed by Hanes

(1971) and by Christensen and Muller (1975) could also have been involved.

The history of disturbance at Dillon Divide may have been a particularly important factor in the regeneration of *Cistus* after fire. The effects of clearing and herbicide use in the 1950's were still evident in 1972. Large, strongly woody chaparral shrubs were not well represented. They had been replaced, in part, by species adapted as invaders on disturbed sites including *Eriogonum fasciculatum, Eriodictyon crassifolium,* and *Bromus rubens*. Because of the "impoverished" condition of the native shrub cover, succession after fire has been quite different than described elsewhere for chaparral (Hanes and Jones, 1967; Hanes, 1971; Vogl and Schorr, 1972). Seedlings and/or resprouting individuals of large chaparral species were notably absent on the burn. The cover was dominated by *Eriogonum fasciculatum, Bromus rubens,* and a number of fire-succession perennial herbs and small sub-shrubs. The absence of regenerating chaparral shrubs and the rather low, open, predominately herbaceous cover appear to be of great benefit to *Cistus*. Even after four years, the vegetative canopy had not become sufficiently dense to limit *Cistus* germination and seedling growth. In a more typical post-fire chaparral succession, it is unlikely that new germinations would have been found beyond the first or second rainy season.

This study is limited to observations of *Cistus* on a single site after one fire. Additional data are needed to define fully the fire ecology of these Mediterranean shrubs in Southern California and to determine cause-effect relationships. Studies are currently underway to obtain such information. Based on the Dillon Divide analysis, however, we suspect that other wildland stands of *Cistus* located on sites with a similar history of mechanical disturbance would have a high potential for recovering after fire and for persisting as part of the vegetative cover. Stands located on relatively undisturbed sites, on the other hand, might be eliminated in the early stages of post-fire succession because of more intense competition with regenerating chaparral shrubs.

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MORPHOLOGICAL EVIDENCE OF HYBRIDIZATION BETWEEN ARCTOSTAPHYLOS GLAUCA AND A. PUNGENS (ERICACEAE)

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Arctostaphylos is a large genus of evergreen shrubs common in western North America. Although species in the group occupy various habitats throughout this region, their greatest diversity is found in the chaparral covered coastal ranges of California. The diversified topography of this area, with its exceedingly complex mosaic of habitats, has doubtlessly contributed to the diversity of the group. Jepson (1939) suggested that much of the variation in this genus was associated with minor climatic differences and was related to the geological history of the region. Similar factors have been proposed by Gankin and Major (1964) to account for the origin of *A. myrtifolia* Parry, and Vasek and Clovis (1976) have also suggested that recent climatic selection has resulted in a complex pattern of variation in *A. glauca* Lindl.

Hybridization has been implicated in explanations of variation in at least 30 species, subspecies, or varieties (Baker, 1932; Eastwood, 1934, 1937; McMinn, 1939; Jepson, 1939; Adams, 1940; Howell, 1955; Munz, 1959; Roof, 1962; Hoover, 1964; Gankin and Hildreth, 1964; Gankin, 1966; Wells, 1965, 1968, 1972). Despite the frequency of reports of suspected hybridization in *Arctostaphylos,* relatively little biosystematic evidence for it has been published. Epling (1947) made the first attempts by quantifying leaf proportions along a transect from a stand of "pure" *A. mariposa* Dudl. in Eastw. to a stand of "pure" *A. patula* Greene. He, and later Dobzhansky (1953), concluded that although hybrids between these two species were abundant and vigorous, both species remained quite distinct along the zone of contact. More recent and complete studies have clearly indicated hybridization between *A. nissenana* Merriam and *A. viscida* Parry (Schmid et al., 1968) and between *A. viscida* and *A. canescens* Eastw. (Gottlieb, 1968). The results of the latter study led Gottlieb to conclude that several species maintained in standard floras are hybrids.

The purpose of this study was to document phenetic patterns of a putative hybrid swarm between *A. glauca* and *A. pungens* HBK., with a view to answering two questions: 1) is there an apparent recombinant type emerging from this population? 2) is there any detectable introgression from one species to the other?

Both *A. glauca* and *A. pungens* are well-defined, easily recognizable, diploid ($2n = 26$), non-burl-forming shrubs that often reach arborescent proportions. *Arctostaphylos glauca* has glaucous ovate leaves 2.0–4.5 cm long with truncate or subcordate bases, petioles 7–10 mm long. Inflorescences are long, narrow, and much branched. Petioles, branchlets, and rachises are typically glabrous and glaucous. Fruits are the largest found in the genus, 12–15 mm in diameter, globose, viscid, and borne on densely glandular pedicels. The exocarp is thin and leathery, there is no mesocarp, and the hard resin-like endocarp is fused into a smooth, solid, apiculate stone enclosing 5–6 seeds. *Arctostaphylos pungens* has narrowly elliptic to almost lanceolate leaves 1.5–3.0 cm long with acute bases, and petioles 3–4 mm long. Inflorescences are short, few branched, and broadened at the tip. Petioles, branchlets, and rachises are densely canescent. Fruits are glabrous, depressed-globose, 5–10 mm broad, and borne on glabrous pedicels. The mesocarp is a mealy pulp and the resin-like endocarp is divided into 5–6 distinct nutlets.

Arctostaphylos glauca is common on dry slopes in chaparral from Baja California through the inner Coastal Ranges to Contra Costa Co., California. *Arctostaphylos pungens* is common from the Mexican Highlands through southern Texas and frequently in higher elevation chaparral and woodland from southern California north to San Benito Co., California (Munz, 1959). In the mountains east of San Diego, *A. glauca* is a common component of chaparral between 600 m and 1500 m. *Arctostaphylos pungens* is frequent in oak woodlands at about 800 m. It becomes more common in chaparral at higher elevations and extends into yellow pine forest up to 2000 m. These two species seldom occur together, although *A. glauca* is found throughout this region in close association with *A. glandulosa* Eastw., a hexaploid, burl-forming shrub.

Study Sites and Methods

The putative hybrid swarm is in Echo Valley (1000 m), ca 8 km N of Descanso, San Diego Co., California. Here *Arctostaphylos pungens* is scattered among *Quercus agrifolia* Neé in flat areas of the valley bottom while *A. glauca* is common on slopes in association with *A. glandulosa, Adenostoma fasciculatum* H. & A., *Quercus dumosa* Nutt., *Ceanothus leucodermus* Greene, and *C. greggii* Gray var. *perplexans* (Trel.) Jeps. In one ravine, on the north-facing slope, *A. glauca* and *A. pungens* occur together with shrubs that combine characteristics of both of these species. This area had not burned in at least 20 years and no obvious disturbance was evident.

Samples were taken by walking a straight line through the center of

the population and collecting a fruiting branch from each of the first 40 shrubs encountered (*J. Keeley 4110-4149*). A similar procedure was used to sample populations of "pure" *A. pungens* and "pure" *A. glauca* except that a sample size of 15 was used. The *A. pungens* population was about 200 m S of the putative hybrid population and the *A. glauca* population was from the east end of Willows Road, The Willows (850 m), ca 9 km SW of Echo Valley. The *A. glauca* population was sampled in Aug 1973 and the *A. pungens* and the putative hybrid populations were sampled in Aug 1974. Vouchers will be deposited in SD.

Each specimen was scored as follows: Ten leaves were randomly selected and removed; leaf length and width and petiole length were measured. The angle (from the midrib) of the leaf base was measured for three leaves. Five inflorescences were selected and the number of side branches recorded, and length of the rachis and width near the tip of the rachis was recorded. Ten fruits were scored as follows: after oven drying to constant weight, the fruits were (1) weighed, the outer pericarp (exocarp and mesocarp) was removed by rubbing on a wire screen, (2) the number of segments into which the endocarp broke was recorded, and (3) these segments were weighed.

The mean value for each of these characters was recorded. Meristic characters (number of inflorescence side branches and number of endocarp segments) were expressed as real numbers. In addition to these quantitative measurements, each specimen was qualitatively scored for: glaucousness (presence of a whitish bloom on the leaves), glandularity, and type of, or absence of, indument on the branchlets, inflorescences, pedicels, and fruits.

Using these data, scatter diagrams were constructed from values for the major distinguishing characteristics. In order to show how shrubs in the hybrid population combined characteristics, a hybrid index similar to that of Anderson (1949) was developed. Rather than sorting quantitative data into discrete groups (e.g., 0 for one parent, 2 for the other, and 1 for intermediates), the following procedure was used. The specimen that had the largest mean measurement for a character was given a value of 1 for that character and all other specimens were scaled proportionately for that character. An *A. glauca* specimen had the largest measurement for most of the characters studied. For those characters in which *A. glauca* did not have the largest measurement, the inverse of the scaled measurement was used. It was thought that this method would make the index more objective as well as more sensitive to gradual changes in the phenetic characters examined.

Ten quantitative characters were used for the hybrid index: leaf length, leaf width/length ratio, petiole length, angle of leaf base, length of inflorescence rachis, width near rachis tip, number of inflorescence side branches, fruit (minus outer pericarp) weight, percent (by weight) of fruit as outer pericarp, and number of endocarp segments. In addition, four qualitative characters (leaf bloom, branchlet indument, glandularity

of pedicels, and glandularity of fruits) were used by assigning values of "0" for *A. pungens*-like, "1" for *A. glauca*-like, and "0.5" for anything else.

Results and Discussion

Recombination of characteristics of *A. glauca* and *A. pungens* in the shrubs from the Echo Valley population is clearly documented in the scatter diagrams (figs. 1 and 2). Nearly all of the shrubs in this population either had characteristics that were intermediate between those of *A. glauca* and *A. pungens* or had combinations of characteristics of both species.

The hybrid index histogram (fig. 3) also illustrates the hybrid nature of the Echo Valley population. Most of the 40 shrubs that were examined at this site had hybrid index values that fell between those of *A. glauca* and *A. pungens*. Also, there was a noticeable scarcity of intermediate values (7–8). Thus, assuming "F_1" individuals would be intermediate between the two parents, it would appear that this population is composed predominantly of backcrosses to either *A. pungens* or *A. glauca*. However, confirmation of this conclusion would require information on the genetics controlling these traits, and this sort of data is difficult to obtain for woody plants.

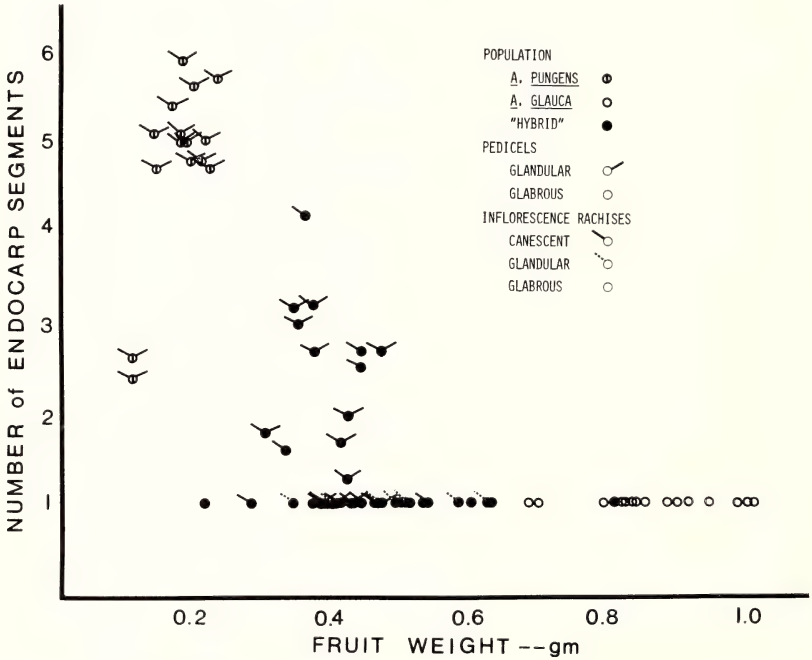

Fig. 1. Pictorialized scatter diagram of the "pure" *Arctostaphylos pungens* population, the "pure" *A. glauca* population, and the putative hybrid population.

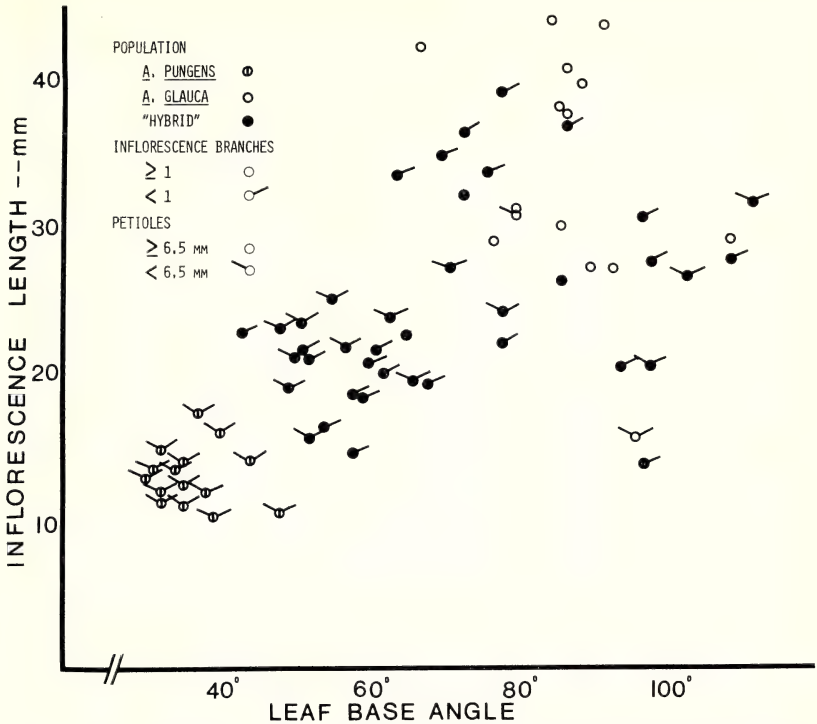

FIG. 2. Pictorialized scatter diagram of the "pure" *Arctostaphylos pungens* population, the "pure" *A. glauca* population, and the putative hybrid population.

The wide distribution of values in the hybrid index histogram (fig. 3) indicates that there are several different recombinant types in the hybrid population. The diversity is even more pronounced than is shown by Figure 3; many of the specimens with the same hybrid index value had very different combinations of characteristics. However, there was a single recombinant type in high frequency with respect to fruit characteristics (fig. 2). A large proportion (ca 70%) of the shrubs in this population had small (pungens-like) fruits with "nearly" or completely fused endocarp segments (glauca-like). This finding is interesting in light of the occurrence of the fused endocarps in the genus; only six other species in the group have this trait. All six have fruits smaller than those of *A. glauca* and are endemic within the range of overlap of *A. glauca* and *A. pungens*.

The clear discontinuity between the *A. pungens* population and the hybrid population in Figures 1, 2, and 3, indicates that there has not been any introgression of *A. glauca* characteristics into *A. pungens*. However, the occurrence of shrubs in the hybrid population with charteristics that fall within the range of variability of *A. glauca,* but have one or two traits of *A. pungens* (figs. 1, 2, and 3), suggests that there has

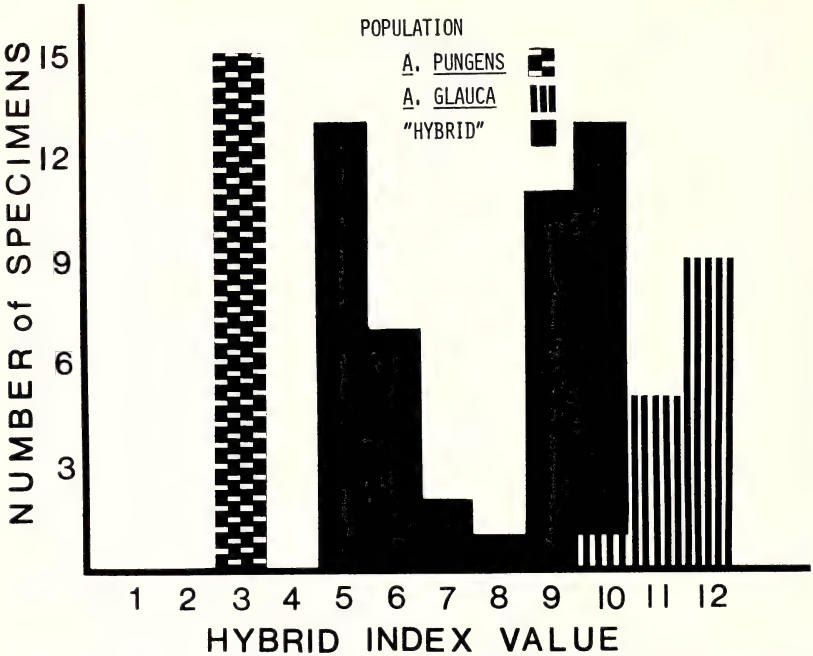

FIG. 3. Histogram of hybrid index values for the "pure" *Arctostaphylos pungens* population, the "pure" *A. glauca* population, and the putative hybrid population.

been introgression of *A. pungens* characteristics into *A. glauca*. In order to examine what effect introgression may have on *A. glauca* away from this immediate area, the following sampling was undertaken. On an east-facing slope about 100 m away, 30 *A. glauca* shrubs were scored for being glauca-like or pungens-like for six characters. Although *A. pungens* is very rare on this slope, only 13 percent of the *A. glauca* shrubs were scored as glauca-like for all six characters. Sixty percent of the shrubs had two or more pungens-like characteristics. Thus, it appears that there is introgression of genes from *A. pungens* into *A. glauca,* and it is detectable away from the site of active hybridization. Whether this is "true" introgression, i.e., a permanent addition of genes into the gene pool (Stebbins, 1959) is not known.

The results of this study indicate that *Arctostaphylos glauca* and *A. pungens* can hybridize when in close proximity to one another. It appears that the Echo Valley hybrid population is composed mainly of backcrosses to both parents. In addition, introgression of *A. pungens* genes into the gene pool of *A. glauca* is suggested by the occurrence of "*A. glauca*" shrubs with one or several *A. pungens* characteristics. Although most of the data from this study can be interpreted by simple explanations such as these, the occurrence of several hybrids with glandular-puberulent petioles, branchlets, and inflorescences, characteristics

of neither *A. glauca* nor *A. pungens* (fig. 2), cannot be easily explained. There are a number of sources by which these traits may have arisen. They may be: (1) the result of new gene combinations, a phenomenon that has been shown for both morphological and chemical characters in some hybrids (Turner and Alston, 1959), (2) the result of hybridization with *A. glandulosa,* a species with glandular petioles, branchlets, and inflorescences and also common at the Echo Valley Site, or (3) the result of introgression with *A. glauca* var. *puberula* J. T. Howell, which differs from var. *glauca* only in its glandular petioles, branchlets, and inflorescences and has recently been reported from several localities near Echo Valley (Keeley, 1975). Alternatively, the origin of var. *puberula* may be linked to one or both of the first two hypotheses. Investigation of this problem would perhaps reveal a great deal about the role of hybridization and introgression in the complicated pattern of variation in this genus.

Acknowledgments

I thank Ms. Sterling C. Keeley and Dr. Samuel B. Jones, Jr., for helpful criticisms and, the latter, for drafting materials, and Mss. Lydia Phillips and Katie Bishop for help in preparation of the manuscript.

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SYSTEMATIC POSITION OF REDFIELDIA (GRAMINEAE)

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In a recent paper reporting on his studies of leaf anatomy among members of the Eragrostoideae, Sutton (1973) indicated that *Redfieldia* Vasey does not belong in this group. As a result of his investigations, he concluded that this genus "should be left in the Festucoideae (tribe Festuceae) as placed by Hitchcock (1935)". Curiously, he did not note that the Grass Manual was revised in 1951 by Mrs. Agnes Chase and that in the later edition, *Redfieldia* is still retained in the Festuceae. It should also be pointed out that Vasey (1887) indicated that it appears to be related to *Festuca*.

Aside from the work of Sutton referred to above, the only other anatomical investigation of *Redfieldia* appears to be that of Decker (1964). In this latter publication the author did not discuss *Redfieldia,* but listed it in his table. Decker indicated that the genus is clearly eragrostoid in all characteristics including those observed in transections of the leaf blade. It is noteworthy that although Sutton listed the above paper in his bibiography, he did not point out that Decker's conclusions were in direct contrast to his own.

Redfieldia was described to accommodate a single species of sand-binding grass originally collected by Hall and Harbour in 1862. It had been recognized as a new species by Thurber, who in 1863 gave it the specific epithet *flexuosum* and doubtfully assigned it to *Graphephorum*

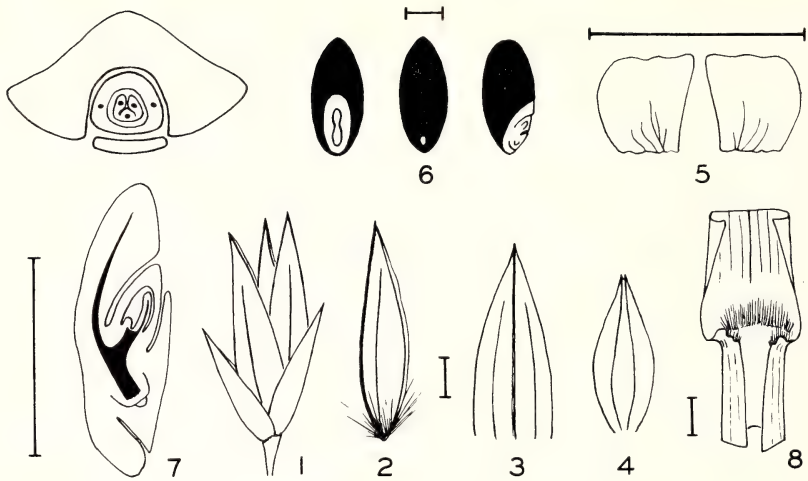
(= *Trisetum*). As indicated above, Vasey pointed out that he considered *Redfieldia* to be allied to *Festuca*. All subsequent authors who follow the traditional system have considered this grass to be a member of the Festuceae.

Apparently, the first publication in which the genus was assigned to the Eragrosteae is that of Pilger (1954); this work is essentially a key and there are no descriptions of genera. Two years later, however, Pilger (1956) gave a detailed description of *Redfieldia flexuosa* in which one finds mention of the 3-nerved lemma and caryopsis with a large embryo and small round hilum. My own investigations of the embryo indicate this same alliance. Decker (1964) had access to my unpublished information on the embryo of *Redfieldia,* but is incorrect in indicating his source as my 1957 paper. Stebbins and Crampton (1961), although making no special comments regarding the characteristics of the plant, also listed it as a member of the Eragrosteae. As already indicated, this placement was supported by the studies of Decker (1964) and has been followed in such recent works as those of Correll and Johnston (1970) and Gould (1968, 1975).

In view of the doubts raised by Sutton regarding the relationships of *Redfieldia,* along with the rather meager information in the literature concerning characteristics of this plant, a detailed study of *R. flexuosa* seems desirable. (A second species, *R. hitchcockii* A. Camus from Madagascar is little known and may not belong to the genus. See Pilger, 1956.)

Redfieldia flexuosa is characteristic of dunes of the central United States, where its ability to hold shifting sand has given rise to the common name "Blowout Grass". It has been reported from eleven states, extending from North Dakota to Texas and westward to Utah and Arizona. Although it has extensive rhizomes, the above ground portion is rather delicate, consisting of slender culms, flexuous involute blades, and a diffuse panicle. The spikelets are 2- to several-flowered, and the glumes are shorter than the lowest floret. The lemmas have three prominent nerves (figs. 1, 2, 3). The flower is typical for the family, having three stamens, a pistil with two feathery stigmas, and two lodicules. The lodicules are truncate and have vascular tissue in the lower half (fig. 5). The caryopsis has a punctate hilum and a relatively large embryo (fig. 6). Sections of the embryo (fig. 7), moreover, reveal that it is of the chloridoid-eragrostoid type, having a formula of P + PF (Reeder, 1957).

Leaves in transection, contrary to the statement of Sutton (1973), show typical chloridoid-eragrostoid structure (fig. 9). The vascular bundle is surrounded by an inner sclerenchyma sheath (endodermis) that in turn is enclosed by an outer sheath of large parenchyma cells. Outside this, the rather scanty mesophyll is arranged in a radiating pattern. Each unit of the leaf that includes a vascular bundle is separated from its neighbor by a row of large parenchyma cells (bulliform

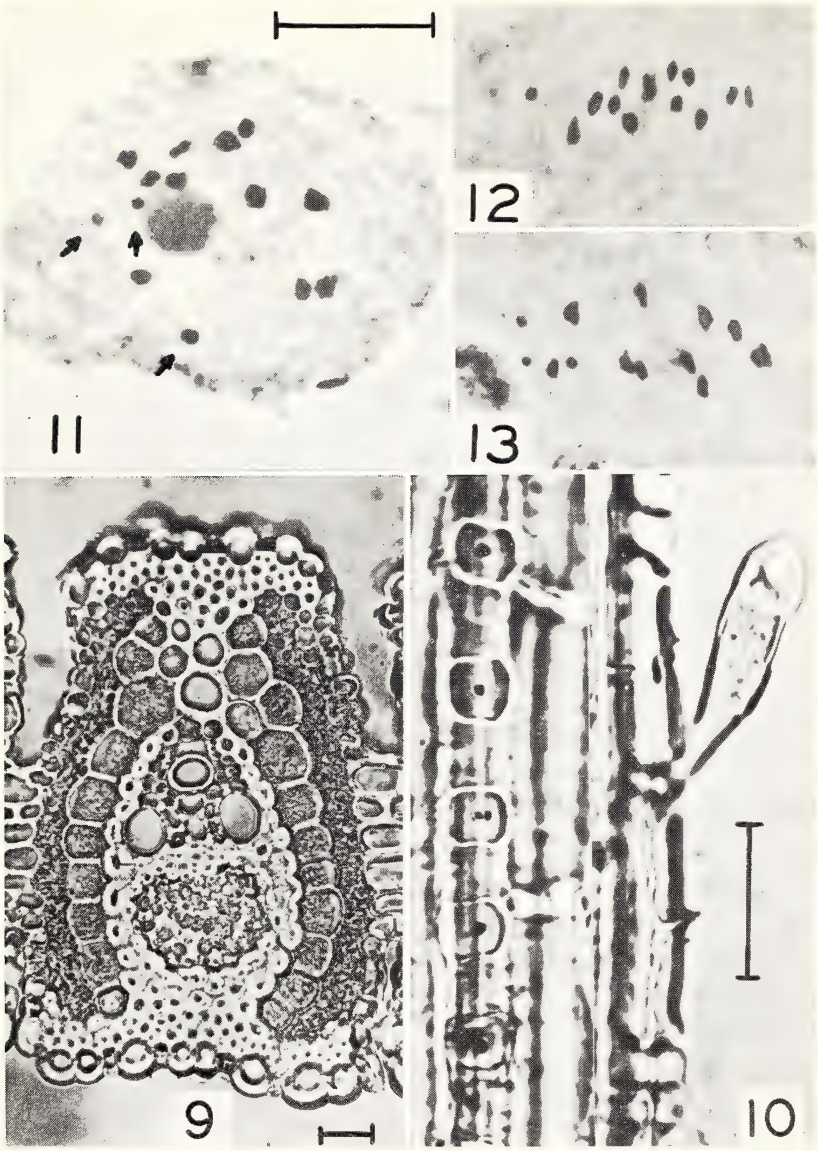


FIGS. 1–8. *Redfieldia flexuosa* (Thurb.) Vasey. 1, Spikelet. 2, Lemma in side view. 3, Lemma opened out to show the three nerves. 4, Palea. 5, Lodicules. 6, Caryopsis in three views showing the embryo and hilum. 7, Embryo in median sagittal section and in transection through the coleoptile region. 8, Ligule. Figs. 1–5 and 8, *J. R. and C. G. Reeder 5398* (RM); 6 and 7, *Rose and Fitch 17095* (US). Scale line = 1 mm.

cells), which extend from the upper to the lower epidermis. Detailed examination of the epidermis reveals two characteristics that are indisputably chloridoid-eragrostoid (fig. 10): (1) the prominent siliceous cells are saddle or double-axe-shaped, and (2) bicellular hairs are of an "ice cream cone" shape, in which the somewhat bulbous apical cell is considerably shorter than the basal one.

Finally, meiotic chromosomes are relatively small (figs. 11–13), and certainly do not at all resemble the large chromosomes characteristic of festucoid grasses. The number ($2n = 25$) is unusual. At diakinesis and metaphase I, 12 II + 1 I (fig. 12) or 11 II + 3 I (figs. 11 and 13) are present. Occasionally in this latter case, one of the bivalents is loosely synapsed. Although evidence presented here is not conclusive, I interpret this number as aneuploid and suggest that the basic number is $x = 10$. Both of my collections came from the "Sand Hills" of Nebraska, and it is possible that this material is cytologically atypical. Chromosome size, and even the number, reported here would seem to exclude *Redfieldia* from any festucoid alliance.

In summary, detailed study of *Redfieldia* indicates clearly that this genus is a member of the Chloridoid-Eragrostoid Group. It was correctly assigned to the Eragrosteae by Pilger (1954). Its eragrostoid characteristics are: lemma three-nerved (figs. 1, 2, 3), ligule ciliate (fig. 8), lodicules trucnate and with vascular traces (fig. 5), caryopsis with punctate hilum and large embryo (fig. 6), embryo with formula P + PF (fig. 7),



FIGS. 9–13. *Redfieldia flexuosa* (Thurb.) Vasey. 9, Transection of leaf through the region of a major vein showing typical chloridoid-eragrostoid anatomy. 10, Epidermis from adaxial surface of leaf blade showing saddle-shaped siliceous cells and bicellular microhair of the "ice cream cone" type. 11–13, First division of meiosis in microsporocytes. 11, Diakinesis, showing 11 II and 3 I. 12 and 13, Metaphase, showing 12 II and 1 I, and 11 II and 3 I respectively. All from collections of *J. R. and C. G. Reeder*: 9 and 10, *5398* (RM); 11, *5406* (RM); 12 and 13, *5404* (RM). Scale line = 20 μm.

chromosomes small, probably $x = 10$ (figs. 11, 12, 13), leaf epidermis with saddle-shaped siliceous cells and bicellular microhairs of the "ice cream cone" type (fig. 10), and leaf anatomy of the Kranz type (fig. 9). The statement of Sutton that the leaf anatomy is festucoid is certainly an error. Perhaps his material was from some festucoid grass mistakenly identified as *Redfieldia*. Since he cites no voucher specimens, this cannot be determined.

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DEVELOPMENT OF MORPHOLOGICAL PATTERNS IN THREE SPECIES OF DELESSERIACEAE

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Small red algae with discrete, leaf-like blades borne on short stipes are inconspicuous, but not rare, in low intertidal and subtidal habitats. In California, such blades with distinct midribs and dentate margins are usually attributed to *Nienburgia andersoniana*, if they are polystromatic. If monostromatic, they are generally referred either to *Anisocladella pacifica* or to one of three species of *Phycodrys*, *P. isabellae*, *P. profunda*, or *P. setchellii* (Abbott and Hollenberg, in press).

The critical distinction between *Phycodrys* and *Anisocladella* is considered to be the way secondary cell rows form—symmetrically and equally on two sides of the central cell row in *Phycodrys* (Kylin, 1923) and unequally in *A. pacifica* (Kylin, 1941). Presumably, this early growth is related to the later development of lateral nerves, which are said to be opposite in *Phycodrys* and alternate or irregularly spaced in other genera where they are present (Smith, 1944; Taylor, 1945, 1957). In practice, however, when collections of *Anisocladella* and *Phycodrys* species are examined, nerves are absent or indistinct in some specimens of both genera. Therefore, venation is not a reliable character for separating such blades into distinct taxa.

Comparison of large numbers of field-collected specimens of *Phycodrys profunda, Anisocladella pacifica,* and *Nienburgia andersoniana* led me to think that characters other than blade morphology might be used to separate the taxa. Since very precise arrangements of cells in apices in these and related genera characterize taxa at several levels in the family (Kylin, 1956), it seemed reasonable to seek non-random development sequences that result in orderly arrangements of thallus parts. If existence of such patterns could be established by study of laboratory-grown thalli, characteristic morphologies might then be recognized in naturally occurring plants.

Materials and Methods

Cultures of *Phycodrys profunda, Anisocladella pacifica,* and *Nienburgia andersoniana* were initiated from apices of freshly collected thalli and grown in 200 ml of an enriched natural seawater medium (Murray et al., 1972) without shaking. Two unialgal *Phycodrys profunda* cultures were maintained for more than a year through several cycles of the life-history and were cloned for experimental procedures. Apices of intertidal *Anisocladella pacifica* and *Nienburgia andersoniana* were snipped at several times during the study, dragged through agar, and exposed to GeO_2. These cultures were grown for shorter periods of time and were seldom unialgal (see Chapman, 1973, for discussion of isolation and culture techniques). Sub-cultures were grown under several combinations of different light periods and intensities (250, 500, 1000 m-c; 8/16, 12/12, and 16/8 hrs. light/dark) and different temperatures (10°, 12°, 16° C). Not all combinations were used for all cultures. These conditions approximated ambient light and temperatures in or near the sites sampled. All cultures were transferred to new media at 3–6 week intervals during experimental periods. Thalli from numerous sites, to 30 m deep, in San Diego County were collected throughout the year; vouchers for all collections, including those that furnished culture inocula, are in the author's personal herbarium. Collections in herbaria elsewhere (AHFH, GMS, UC) were examined.

Results

Early cell divisions: Cells close to primary apical cells in *Phycodrys*

profunda and *Anisocladella pacifica* are drawn in Figure 1. My observations of *Nienburgia andersoniana* apices agree with those of Nienburg (1908). In thalli of all three species, the central and pericentral cells, then the secondary and higher order cell rows, form in a similar way. The apical cells that first protrude from the margins are at different distances from the primary apical cell on the two sides of the blade apex, rather than being equidistant from the apex and opposite. These early dentations, and the nerves that appear later, tend to alternate in *Phycodrys profunda* and *Anisocladella pacifica*. Nerves are not formed in *Nienburgia* species.

As growth continues, however, development of structures from thallus margins is dissimilar in the three species. Laboratory-grown blades and axes are shown in Figures 2–4. These can be compared with field-collected plants in Figures 5–7.

Phycodrys profunda: On cultured thalli, haptera (fig. 2 a) form directly from marginal cells of the blades and commonly terminate in uniseriate, multicellular rhizoids (fig. 2 b). Before rhizoids form, the haptera appear as smooth-tipped, tapered, terete spines (fig. 2 d). Haptera and rhizoids form without direct contact between the thallus and culture dish surfaces. A narrow blade occasionally grows from the side

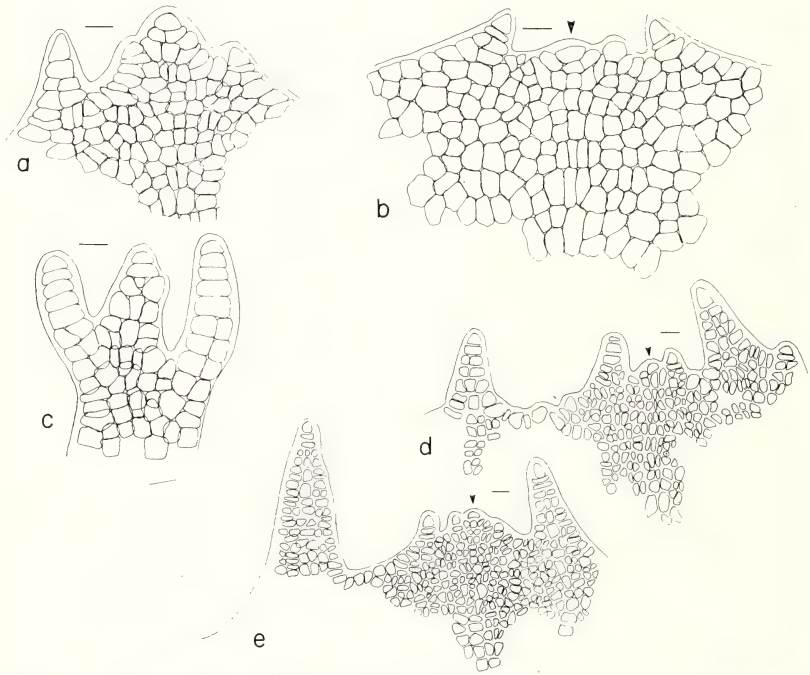
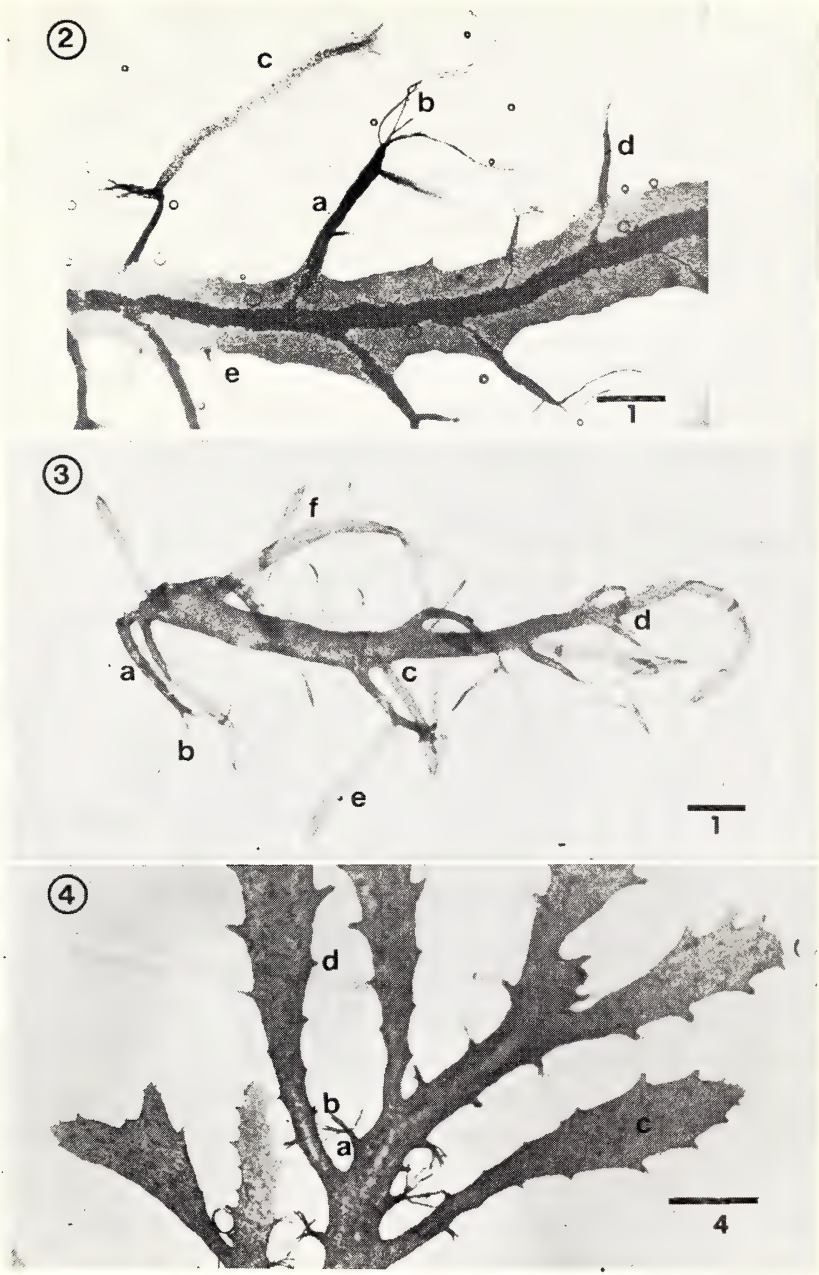


FIG. 1. Arrangement of cells near primary apical cell in *Anisocladella pacifica* (A–C) and *Phycodrys profunda* (D–E). A,B,D, and E, blades. C, prostrate axis. Scale = 15 μm; Arrows = primary apical cells.



FIGS. 2–4. Laboratory-grown thalli of algae. 2, *Phycodrys profunda*. 3, *Anisocladella pacifica*. 4, *Nienburgia andersoniana*. Scales are in mm; a = hapteron, b = rhizoids, c = secondary blade, d = spine, e = adventitious blade, f = branch axis.

(fig. 2 c) of an older hapteron after terminal rhizoids have formed. These secondary blades develop midribs, nerves, and marginal haptera in the same manner as do primary blades. Secondary blades do not grow directly from margins of primary blades during this initial growth period. On some older thalli, very narrow blades are initiated adventitiously from blade margins (fig. 2 e) in positions apparently unrelated to structures already present. These bladelets remain small and unbranched.

Haptera and secondary blades are borne in the same way on field-collected thalli. Tips of haptera (fig. 5 a), fastened by rhizoids (fig. 5 b) to a substrate, become torn when the plant is removed. Lateral blades on haptera are rare (fig. 5 c). Reproductive structures that correspond to those on the primary blade can occur on secondary blades. Secondary

FIGS. 5–7 Field-collected thalli of algae. 5, *Phycodrys profunda*. 6, *Anisocladella pacifica*. 7, *Nienburgia andersoniana*. Scales are in mm; a–f as in Figures 2–4.

blades do not occur directly on margins of other blades. Primary blades are subtended by short terete stipes that branch from other stipes or grow from small, discrete holdfasts. Nerves are more often alternate than opposite, but their arrangement varies. No prostrate axes were found. Haptera can develop from the point on the margin where a nerve terminates, but often the positions of the two are unrelated. On many specimens the marginal projections are undifferentiated, appearing as short dentations or spines (fig. 5 d).

Anisocladella pacifica: Width of blades varied in cultured thalli. I was often uncertain whether to interpret a given region as blade or axis. After forming narrow thallus parts for several weeks, an apex may produce an expanded, more blade-like part. Photographic records of individual thalli show that haptera with rhizoids (fig. 3 b) develop first in positions that alternate on opposing sides. Very small spines (fig. 3 d), or narrow dentations, form very close and just distal to haptera. These later grow out to become secondary blades (fig. 3 c), or they may remain narrow as they branch and function as axes (fig. 3 f). Very rarely, blades grow from lateral positions on haptera (fig. 3 e).

On axes of field-collected thalli (fig. 6), haptera and erect blades (or axial branches) are in pairs in a definite pattern, or one or both of the structures may be an undifferentiated spine. Where both structures are developed, the hapteron is always proximal and the blade distal. These pairs grow from opposite edges of erect and prostrate axes in an alternate arrangement. All axes terminate in blades. On axes appressed to substrates, haptera (fig. 6 a) are fastened to the substrate, presumably by means of terminal rhizoids (fig. 6 b), and the adjacent structure is a simple spine (fig. 6 d). Where the axis bears blades (fig. 6 c) or other axes, a spine in a proximal position represents the incipient hapteron. Blade margins typically are dentate. The extent to which nerves are developed and arrangement of nerves vary.

Nienburgia andersoniana: On laboratory-grown thalli, haptera and secondary blades develop on margins of both prostrate axes and erect blades. Regularly spaced haptera with rhizoids (fig. 4 a,b) develop alternately on one then on the other edge before blades (fig. 4 c) appear in between the haptera.

Plants collected in the field (fig. 7) exhibit the same alternate arrangements of marginal structures on all thallus parts. Spines frequently occur in place of either haptera or blades. A branch axis can replace a blade anywhere on the thallus.

Reliability of patterns: These patterns in the way blades and haptera are arranged in each taxon were a reliable way to distinguish the three species, although on some damaged thalli they are difficult to recognize. Each of the patterns proved to be species-specific, and their development was unaffected by different regimes of light and temperature when thalli were grown in the laboratory.

Discussion

In *Phycodrys profunda,* early development of cell rows and, later, the irregular formation of nerves, resemble comparable stages in the *Nienburgia* and *Anisocladella* species and do not distinguish thalli of one species from another. These two aspects of growth, and the positions of marginal dentations, are asymmetrical on the two edges of the blades. For *Nienburgia andersoniana* and *Anisocladella pacifica* apices, these observations agree with earlier descriptions of these species (Nienburg, 1908; Kylin, 1941) but disagree in respect to the characterization presently accepted for *Phycodrys* species (Kylin, 1956).

Kylin considered that the symmetrical development he ascribed to *Phycodrys sinuosa* (Kylin, 1923) was significantly different from that of *Anisocladella, Nienburgia,* and other genera in the same group. Since *P. sinuosa* (=*P. rubens*: see discussion of nomenclature in Dixon, 1964) is the type species, this characterization has been extended to other species of the genus (Kylin, 1956). Rosenvinge (1931) stated, in support of Kylin's study, (since) "the two initial segments of a segment always behave in the same manner, the lobes are always opposed". Writers of various algal floras (see above) mention opposite nerves in describing the genus, perhaps following the opinion of Kylin rather than as a result of critical evaluation of the character.

Phycodrys rubens on both sides of the north Atlantic is a rather common species and *P. setchellii* in the Pacific is very similar. In both, nerves are often strikingly and regularly opposite, but thalli of each species can be found in which the arrangement of nerves varies in the same ways as described here for specimens of *P. profunda.* Dawson (1962) did not mention apical anatomy in *P. profunda* but he did refer to "opposite veins". *Phycodrys isabellae* nerves were said to be opposite but often weakly developed or lacking (Norris and Wynne, 1968). Many other species attributed to the genus are seldom collected and known only from scant material. Arrangements of nerves other than precisely or even approximately opposite are associated with certain of these. Taylor (1945) stated that *P. elegans* (as *P. pulchra*) possesses "irregularly alternate lateral veins". Nerves of *P. amplissima* are arranged very irregularly (Dawson, 1962). Wynne (1970) characterized *Phycodrys* blades in general as being "heavily veined" but he did not use "opposite" in this context. It may be that the criteria of equally developed, opposite secondary cell rows and the perhaps concomitant development of symmetrical nerves cannot be strictly applied to any species of *Phycodrys* when numerous collections are studied. The proportion of bilaterally symmetrical blades certainly varies between, as well as within, species. The secondary cell rows on opposite sides of the midrib are frequently unequal in *P. profunda*; since one of the two lateral pericentral cells in each segment is always formed before the other, the two apical cells of opposing cell rows form at different times, and it seems reasonable that this inequality might persist in subsequent development.

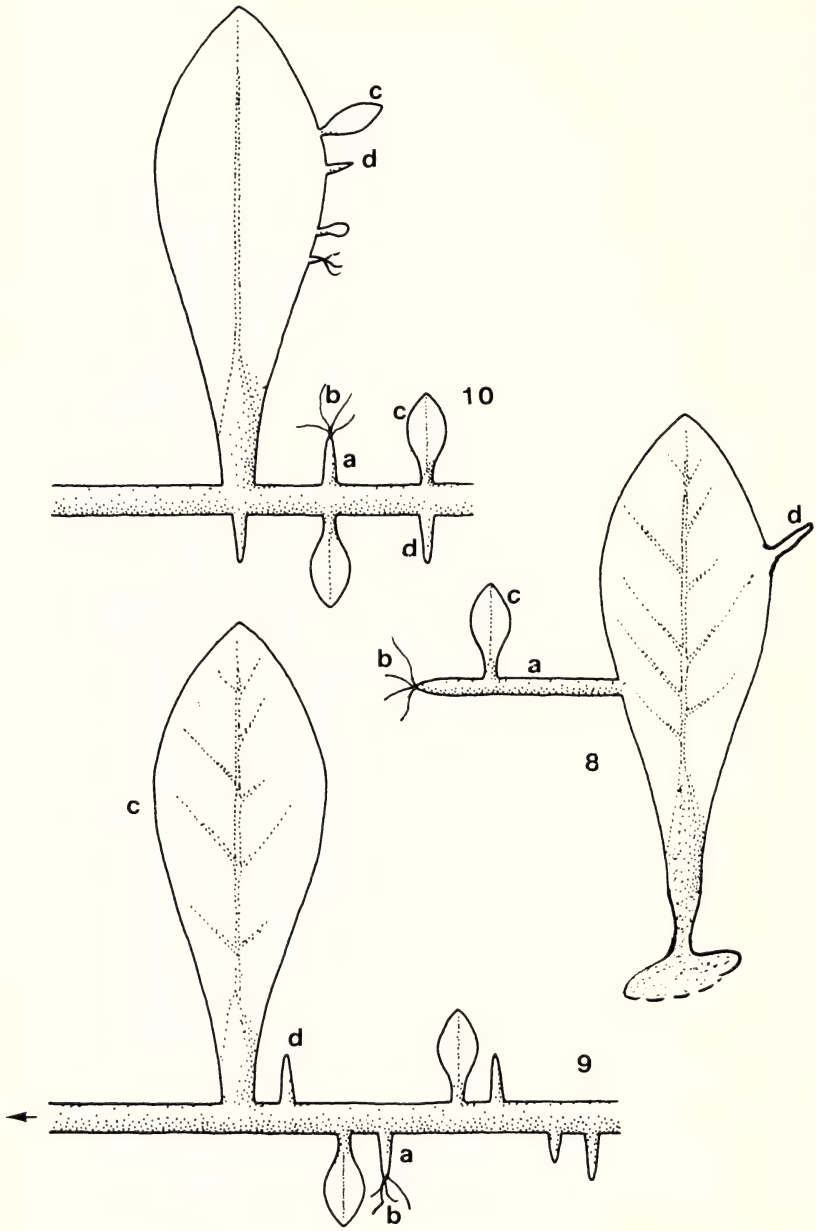
Marginal haptera on blades, such as characterize *P. profunda,* are found infrequently on *P. setchellii.* On blade margins of *P. isabellae,* there are "terete rhizoid-bearing processes that may form secondary attachments" (Norris and Wynne, 1968). Similar structures occur on blades of *P. lucasana* (Dawson, 1962). Lateral blades, from the sides of haptera, are rarely seen, but evidently the potential for their development exists in *P. profunda* and *P. setchelli* at least. Specimens of many species of *Phycodrys* have numerous secondary bladelets borne directly on margins of larger blades. Most of these species are larger than *P. profunda* so blade margins would be less likely to be in contact with substrate surfaces to which haptera might attach. Descriptions of these species do not mention prostrate axes. The absence of regularly branched prostrate axes possibly can be shown to demarcate *Phycodrys* species from species of other genera with haptera and blades arranged in orderly ways on prostrate axes.

Use of the patterns described here as distinguishing three species (cf. figs. 8–10) might be extended to the generic level. Although limited, available information supports use of the patterns for *Nienburgia* and *Anisocladella.* The only parts of *A. serratodentata* (the type and only other species of *Anisocladella* known) that have been described are dentate blades (Skottsberg, 1923; Kylin, 1956; as *Delesseria serratodentata,* Kylin and Skottsberg, 1919). In discussing *Nienburgia prolifera,* Wynne (1970) definitely alludes to an arrangement of parts such as shown here for *N. andersoniana* (fig. 10). Descriptions of species from South Africa (*Nienburgia serrata,* Papenfuss, 1956, as *Nitophyllum serratum* in Suhr, 1836; *Nienburgia pinnatifida,* Papenfuss, 1968, as *Nitophyllum pinnatifidum* in Suhr, 1834) do not mention prostrate axes or haptera. European species are not known (P. S. Dixon, pers. comm.). Thus, there are no species in either genus that can be shown to lack the patterns described here or to have different arrangements of branches.

The development described in the three species studied here can be interpreted in terms of two kinds of branches that are formed in regular sequences. A hapteron that ceases to elongate when terminal rhizoids form is a determinate branch. It does not repeat its own development to form new haptera. Blades are equivalent to axes insofar as both are indeterminate branches that are capable of unlimited growth behind a persistent primary apical cell. These branches repeat the developmental sequences by which they were formed. Certain marginal cells on indeterminate branches (blades and axes) can become apical cells of either determinate or indeterminate branches; determinate branches form only lateral indeterminate branches. The two types of branches form in predictable sequences while the thallus is growing and their final arrangement is orderly and distinctive in each species.

Other observations suggest that different apical cells on margins have different potentials for rates and orientation of cell division. As far behind the apex as cell rows can be traced clearly, neither rows of higher order than secondary nor accessory rows derived from intercalary cells

of the central cell row grow beyond the margins. The potential to convert to growth as primary apical cells may be restricted to apical cells of sec-



FIGS. 8–10. Diagrams of branching patterns in algae. 8, *Phycodrys profunda.* 9, *Anisocladella pacifica.* 10, *Nienburgia andersoniana.* Arrow indicates direction of apex; a–f as in Figures 2–4.

ondary cell rows. The space between adjacent marginal dentations increases with distance behind the apex, corresponding to the development of other rows of cells between secondary cell rows. In these genera, only cells of secondary cell rows divide perpendicularly to the plane of the blade to produce thickened nerves. The regular spacing of determinate and indeterminate branches along prostrate axes in *Anisocladella pacifica* and *Nienburgia andersoniana* and the tendency of haptera to be aligned with nerves in *Phycodrys profunda* support the conclusion that differentiation of marginal apical cells is rather precisely regulated.

Marginal branching patterns have proved to be reliable for recognition of the three species studied here. Apart from the taxonomic usefulness, the distinctions also imply that regulation of morphogenesis extends to regions of the thallus far removed from the primary apex and persists throughout the growth of the thallus.

Acknowledgments

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ARMILLARIA (TRICHOLOMATACEAE, AGARICALES) IN THE WESTERN UNITED STATES INCLUDING A NEW SPECIES FROM CALIFORNIA

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Armillaria Kummer has, to a large extent, been neglected by agaricologists, and no extensive treatment of North American species has appeared since that of Kauffman (1922). Prior to his publication, the only available treatment of the genus was that of Murrill (1914). Both of these works are difficult to use because many species that no longer belong in *Armillaria* are included. The common occurrence of a new species, described below, as well as the frustration resulting from the inability to identify numerous collections belonging to this genus, stimulated us to devote some time to the taxonomy of the species that occur in California, and, to a lesser extent, to those occurring in western United States. Results of this investigation along with a key to western North American Armillarias are presented below. Colors in quotations are from Ridgway (1912).

Armillaria, as conceived by us, includes those white-spored mushrooms that have attached rather than free lamellae, a centrally attached stipe, and a partial veil that usually forms an annulus. Based on their frequency of appearance, two groups of *Armillaria* species can be recognized in the United States west of the Rocky Mountains. One group, which includes *A. mellea, A. ponderosa, A. zelleri, A. albolanaripes,* and *A. olida,* fruits every year and usually in considerable abundance. The second group contains species that appear only sporadically and are rare, particularly in California. Included in this group are *A. caligata, A. subcaligata, A. robusta, A. luteovirens,* and *A. viscidipes.*

Key to the Armillarias of Western United States

a. Lamellae decurrent or nearly so; basidiocarps lignicolous or growing in the close vicinity of wood, often cespitose ..... 1. *A. mellea*

a. Lamellae adnate or adnexed; basidiocarps usually not lignicolous or cespitose ..... b.

b. Pileus yellow at least when young, some may darken with age ..... c.

b. Pileus white, orange, or reddish, sometimes colored otherwise but not yellow ..... d.

c. Pileus noticeably scaly at least on the margin, stipe with similar scales; basidiocarps not darkening to brown or vinaceous with age ..... 2. *A. luteovirens*

c. Pileus glabrous or appressed fibrillose when young, usually noticeably appressed fibrillose when old; pileus surface darkening to brown, vinaceous, or olive with age ..... 3. *A. albolanaripes*

d. Pileus distinctly viscid or subviscid when wet (viscidity may be apparent only when young) ..... e.

d. Pileus moist or dry, but not distinctly viscid ..... f.

e. Pileus orange to orange-red, with olive stains; stipe with similarly colored scales; odor strongly farinaceous ..... 4. *A. zelleri*

e. Pileus pallid to whitish or pale buff; lacking orange-colored stains or scales; odor strongly subalkaline ..... 5. *A. viscidipes*

f. Pileus brown to grayish brown or pale olive, stipe white, glabrous to to silky fibrillose; annulus fibrillose, sometimes disappearing; odor strong, unpleasant, of rotting white potatoes; subalpine in distribution ..... 6. *A. olida*

f. Basidiocarps not with the above characters ..... g.

g. Pileus white or whitish, usually with buff or rust-colored stains or spots; stipe with strongly developed, sheathing veil; odor spicy, aromatic ..... 7. *A. ponderosa*

g. Basidiocarps not as above; pileus usually darker colored (brown to reddish brown) ..... h.

h. Pileus reddish to reddish brown; lamellae pallid, with reddish spots ..... 8. *A. robusta*

h. Basidiocarps not as above; pileus brown to dark brown ..... i.

i. Spores 6.0–7.5 by 5 μm ..... 9. *A. caligata*

i. Spores 9.6–12.0 by 7.8–9.6 μm ..... 10. *A. subcaligata*

1. Armillaria mellea (Vahl ex Fr.) Kummer

This species, which is abundant throughout most of North America, is characterized by decurrent to subdecurrent lamellae, brown, fibrillose scaly pilei, typically lignicolous habitats, and often large clusters of basidiocarps. Its macroscopic characters are highly variable and it is sometimes difficult to identify. At times it is parasitic and attacks the roots of a wide range of hardwood trees and shrubs causing considerable damage. Often, however, it is saprophytic on both hardwoods and conifers.

Armillaria mellea and *Clitocybe tabescens* (Scop. ex Fr.) Bres. and some less common species of both genera have been placed in *Armillariella* by many (Singer, 1975). This segregation is based largely upon the lack of amyloid spores and occurrence of a bilateral type of lamellar trama in these taxa. The characters are supplemented, at least in some species, by the development of conspicuous black rhizomorphs and by the lignicolous habitat. Segregation may be the proper disposition of these taxa; however, because the amyloidity of the spore wall is weak or absent in other Armillarias and because the bilateral nature of the lamellar trama is usually apparent only in very young basidiocarps and often easily overlooked even then, we prefer to keep these species in *Armillaria* for the present.

2. Armillaria luteovirens (A. & S. ex Fr.) Gill.

Not yet known from California, this *Armillaria* is rare to infrequent throughout western North America, and we have seen fresh material only from Utah. Smith (1975) published an excellent photograph made from specimens collected in Oregon. This taxon is most likely to be confused with *A. albolanaripes*. A white form, *A. luteovirens* f. *alba* A. H. Smith, occasionally occurs along with the more typical yellow specimens (Smith and Walters, 1947).

3. Armillaria albolanaripes Peck

This agaric is common in both the coastal and alpine regions of California as well as throughout most of the western United States. It is easily recognized by the rather large, soft, white, cottony scales on the surface of that part of the stipe below the annulus and the yellow pileus, which develops olive or brownish to vinaceous colors when old or dried. Furthermore, the cuticle frequently forms rather large, fibrillose scales, which are often rather conspicuous with age. It may be confused with *A. luteovirens* (q.v.) or *A. zelleri* (q.v.).

4. Armillaria zelleri Stuntz & A. H. Smith

Armillaria zelleri appears to be confined to the western United States, occurring from Washington to California along the coast and inland as far as Arizona. It is distinguished by the viscid to glutinous pileus, which is orange to orange-red, often developing olivaceous stains or spots with age, the orange to orange-red scales on the stipe, and the strong farinaceous odor. It is distinguished from the somewhat similarly colored *A. robusta* by the viscid pileus and stipe. *Armillaria zelleri* is also quite similar in appearance to some species of *Tricholoma* such as *T. aurantium* (Schaeff. ex Fr.) Ricken and *T. subannulatum* Batsch & Bres.; however, unlike these species, it has an annulus and adnate to adnexed lamellae.

5. Armillaria viscidipes Peck

This species of *Armillaria* is not yet known from California and apparently has been recorded from western North America only by Kauffman(1925; Hotson, 1940) who found it in the vicinity of Mount Hood in northern Oregon. The only other known locality is New England. This

species has a very thin but distinct viscid layer on the pileus and a similar layer on that part of the stipe covered by the universal veil. In addition, it was characterized by Kauffman as having a "strong subalkaline odor". Herbarium material of this species from the eastern United States possesses the viscid layers and is rather reminiscent of *A. ponderosa* in color and stature. It is possible some collections of *A. viscidipes* have been misdetermined as *A. ponderosa*.

6. **Armillaria olida** Thiers & Sundberg, sp. nov.

Pileus 7–15 cm latus, e convexo planus, siccus vel udus, glaber vel subtomentosus, albus demum bubalinus vel brunneus, saepe olivaceotinctus. Contextus 0.5–1.5 cm crassus, albus. Sapor farinaceus, odor ingratus. Lamellae albae, adnatae vel adnexae. Stipes 8–14 cm longus, 2.0–3.5 cm crassus, aequalis vel subclavatus, albus, super annulum glaber vel sericeo-fibrillosus, infra annulum fibrillosus vel fibrillososquamosus. Annulus albus, fibrillosus. Sporae 10.5–12.5 μm longae; 5.0–6.7 μm crassae, ellipsoideae. Cystidia nulla. Cuticula pilei ex hyphis intertextis composita. Basidiocarpi gregarii in humo sub arboribus coniferis.

Holotypus: California, El Dorado Co., Crystal Basin Recreation Area, 6 May 1972, *H. D. Thiers 28816* (SFSU).

Pileus 7–15 cm broad at maturity, convex to broadly convex when young, typically becoming plane to shallowly depressed with age, often with the margin becoming elevated and highly irregular in outline; surface dry to moist but not viscid, dull, glabrous to somewhat tomentose, usually appearing streaked or appressed fibrillose when old, and usually with a thin, white, filamentous layer on the disc, at least when young; when very young, or when covered with litter, surface white or whitish, with age and upon exposure to light becoming fuscous to brown ("mikado brown" to "buckthorn brown"), sometimes much paler ("clay color" to "warm buff"), and frequently with olive or grayish shades; not changing color when bruised; margin incurved when young, becoming decurved at maturity, entire.

Context 0.5–1.5 cm thick, white, unchanging or darkening slightly when exposed. Taste farinaceous. Odor very strong, unpleasant, and strongly reminiscent of rotting white potatoes.

Lamellae adnate to adnexed when young, seceding and often appearing free or deeply notched with age; white when young, usually assuming a pinkish cast with age; close to subdistant, broad, thick, margin entire, concolorous; 2–3 tiers of lamellulae.

Stipe 8–14 cm long, 2.0–3.5 cm broad at the apex; equal to somewhat enlarged at the base or subclavate; surface white to pale buff ("pale olive buff") during all stages, unchanging when bruised; glabrous to silky appressed fibrillose above the annulus, appressed fibrillose to fibrillose scaly below; dry; solid, context white, unchanging when exposed. Annulus median to superior, fibrillose and sometimes poorly developed but always present, white but staining brown or orange when bruised.

Spores white in deposit, 10.5–12.5 by 5.0–6.7 μm, ellipsoid, apiculus eccentric, walls thin, smooth, hyaline in KOH, inamyloid (pale yellow). Basidia 4-spored, clavate, hyaline in KOH, 23–30 by 8–10 μm, siderophilous granules (red-staining granules when mounted in acetocarmine) absent; no cystidia present; lamellar trama parallel to obscurely interwoven, hyaline, hyphae 2–4 μm in diam.; pileus trama homogeneous, interwoven, hyphae 3–5 μm in diam.; cuticle differentiated as a layer of interwoven, gelatinous hyphae (an ixotrichodermium), 200–300 μm broad, hyaline in KOH, hyphae 2–4 μm in diam. No caulocystidia seen. Clamp connections absent.

Habit, habitat, and distribution: Solitary to gregarious and often buried in humus under conifers (*Abies* and *Pinus*) at elevations of 1200 m and above throughout the Sierra Nevada and less commonly in the coastal ranges in central and northern California.

Material studied: Calaveras Co.: *Thiers 16756*. El Dorado Co.: *Thiers 28818* (Holotype), *30911, 32229, 34050; Sundberg 1875, 1936*. Fresno Co.: *Thiers 34218*. Mendocino Co.: *Toren 1266*. Nevada Co.: *Thiers 32199*. Sierra Co.: *Thiers 25360, 28938*. Siskiyou Co.: *Thiers 25407*. Tuolumne Co.: *Thiers 19488, 25321, 30915*. All in SFSU.

Discussion: The inamyloid spores of *A. olida* places it in sect. *Ponderosa,* but its relationship with other species remains unclear. Also, the stature and color of the pileus are somewhat suggestive of species in *Lyophyllum* sect. *Constricta;* however, there are no siderophilous granules in the basidia.

7. Armillaria ponderosa (Peck) Sacc.

This large, sturdy mushroom occurs throughout the western states at all elevations and often in considerable abundance. It is eagerly sought as an esculent and is sometimes exported to other countries. In addition to the robust nature of the basidiocarp, it is characterized by the white or whitish pileus, which often has brown or rust-colored stains, a sheathing, well developed annulus, a spicy, aromatic odor, and globose to subglobose spores. *Armillaria caligata* and *A. subcaligata* A. H. Smith & Rea, with which it might possibly be confused because of the similarity of odors, are distinguished by the much darker colored pilei, while *A. viscidipes*, which has a somewhat similarly colored pileus, is viscid. *Armillaria arenicola* Murr. and *A. magnivelaris* (Peck) Murr., both reported from the west coast, are apparently synonyms of *A. ponderosa,* but material of these species has not been seen by us.

8. Armillaria robusta Fr.

This species is not known from California. The only record of its occurrence on the west coast of the United States is a somewhat tentative identification made by A. H. Smith of a collection from Olympic National Park in Washington. It has been found by one of us (HDT) in the coniferous forests of northern Arizona. *Armillaria robusta* is very similar in color and general appearance to *A. zelleri,* and the two species are likely to be confused as evidenced by Zeller's (1938) report

of its presence in Oregon, which, according to Smith (1949), was based upon a collection of *A. zelleri.* The only major macroscopic difference between the two species is the absence of a viscid layer on either the pileus or stipe of *A. robusta.*

9. ARMILLARIA CALIGATA Fr.

This *Armillaria* has not been reported from California but probably occurs here. At present it is known with certainty only from the Puget Sound area, Washington (McKenny and Stuntz, 1971). *Armillaria caligata* has an odor like that of *A. ponderosa* and is somewhat similar to it macroscopically. The pileus surface of *A. caligata,* however, has rather large, dark-colored, appressed fibrillose scales and the basidiocarps are smaller and more delicate. *Armillaria subcaligata,* which does occur in California, is similar to *A. caligata* except that it has larger spores and bilateral lamellar trama (Smith and Rea, 1944).

10. ARMILLARIA SUBCALIGATA A. H. Smith & Rea

Fresh material of this species has not been seen by either of us. It is apparently very rare, and, to the best of our knowledge, is known only from the type locality in the Santa Barbara region of California where it was collected in a "dry lawn" (Smith and Rea, 1944). For additional comments see the discussion under *A. caligata.*

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ANNOUNCEMENT OF MEETING.—On October 23–24, 1976, the California Botanical Society will again sponsor a series of papers contributed by graduate students, to be held at the University of California at Santa Barbara. Papers from all botanical fields are being solicited. Members and non-members of the Society, both professional and non-professional, are invited to attend. An advance registration fee of $2.00 is requested. For registration forms or additional details, contact Dr. Dale M. Smith or Ms. Ann Howald, Department of Biological Sciences, University of California, Santa Barbara 93016.

SEDUM SPATHULIFOLIUM (CRASSULACEAE), NEW TO THE SANTA MONICA MOUNTAINS, CALIFORNIA.—The range of *Sedum spathulifolium* Hook. ssp. *yosemitense* (Britton) Clausen has been extended approximately 60 km southwest: California, Los Angeles Co., Goat Buttes overlooking Malibu Creek, steep, northwest-facing, rocky slope, 215 m, *Gordon et al. 1000* (SFV). The plants were found in close proximity to *Allium peninsulare* Lemmon, *Dudleya lanceolata* (Nutt.) Britt. & Rose, *Phacelia imbricata* Greene, and *Clarkia cylindrica* (Jeps.) Lewis & Lewis. The surrounding community is chaparral, grading into a riparian community along the creek.

The previously reported range for this taxon is in the San Gabriel and San Bernardino Mountains at 760–2280 m and north through the Sierra Nevada to Eldorado Co. (Clausen, *Sedum of North America north of the Mexican Plateau,* 1975). No member of this genus has heretofore been recognized as indigenous to the Santa Monica Mountains (Raven and Thompson, *Flora of the Santa Monica Mountains, California,* 1966).—THOMAS R. GORDON and MICHAEL H. GRAYUM, Department of Biology, California State University, Northridge 91330.

RANGE EXTENSIONS FOR LOWER VASCULAR PLANTS IN ARIZONA.—Examination of specimens of lower vascular plants in the seven major Arizona herbaria (ARIZ, ASC, ASU, ASUF, DES, GCNP, and MNA) has revealed new range extensions including two first records for Arizona. New county records are also reported. These records supplement the distributional data in *Arizona flora* (Kearney et al., 1960) as well as more recent published reports.

Adiantum pedatum L. Yavapai Co., Montezuma Well, 1372 m, 16 Apr 1950, *Kleiner s.n.*, ASC. First county record. Previously known in Arizona from a few localities in Coconino Co., one in Cochise Co., and one in Gila Co. (Kearney et al., op. cit.).

Azolla filiculoides Lam. Cochise Co., Babocomari Ranch area, 30 Sep 1967, *Minckley and Taylor s.n.,* ASU. Maricopa Co., Granite Reef Dam, 16.1 km NE of Mesa, 3 Feb 1957, *Mounts s.n.*, ASU. Pinal Co., Aravaipa road, 17.5 km E of Rte 77, SE of Winkleman, 4 Feb 1967, *Lehto et al. 7730,* ASU. All first county records. Previously reported from Mohave, Pima, Santa Cruz, and Yuma Cos. (Kearney et al., op. cit.).

Cheilanthes villosa Davenp. ex Maxon. Coconino Co., Grand Canyon National Park, Havasu Canyon, Mooney Falls, dry shaded limestone cliff, 792 m, 10 Nov 1952, *Blakely 1605,* DES. First county record. This station, the northernmost for the species in North America, represents a northward range extension of ca. 370 km from previously known Arizona localities. The species had been reported from Cochise, Maricopa, Pima, Santa Cruz, and Yuma Cos. (Kearney et al., op. cit.).

Marsilea vestita Hook. & Grev. (*M. mucronata* A. Br.). Santa Cruz Co., Charco south of Lochiel–Parker Canyon Lake road, ca. 5.6 km NE of Lochiel, ca. 1432 m, 10 Oct 1965, *Niles, Reese, and Stone N698,* ARIZ. Yuma Co., Alamo Crossing, Bill Williams River, 457 m, 14 Apr 1962, *Wetherill and Long s.n.,* MNA. First county records. Reported previously from scattered localities in other counties throughout the state (Hevly, Plateau 33:88–92, 1961).

Phanerophlebia auriculata Underw. Yavapai Co., Boynton Canyon, W of Sedona, 30 Oct 1954, *Deaver 4788,* ASC. First county record. This station, the northwesternmost for the species in North America, represents a range extension of ca. 160 km from the nearest previously reported Arizona locality. Previously reported from scattered localities in Cochise, Graham, Pima, Pinal, and Yuma Cos. (Kearney et al., op. cit.) and Gila Co. (Pase and Johnson, Flora and vegetation of Sierra Ancha Experimental Forest, Arizona, U.S.D.A. Forest Service Research Paper RM-41, 1968).

Selaginella arizonica Maxon. Yavapai Co., Bradshaw Mountains, Turkey Creek, 19 Jan 1957, *Wetherill s.n.,* MNA. First county record. This is the northwesternmost known station for this species representing a range extension of ca. 60 km from previously reported localities in Maricopa Co. Previously known throughout southern Arizona.

Selaginella densa Rydb. var. *densa.* Apache Co., White Mountains, Twenty-four Draw, 2670 m, 13 Jul 1958, *Haskell s.n.,* MNA. First state record; see discussion below.

Selaginella densa Rydb. var. *scopulorum* (Maxon) Tryon. Apache Co., White Mountains, Mt. Ord, along West Fork of Ord Creek, 3261 m, 15 Aug 1968, *Dybdahl R743,* MNA. Second state and county record. This variety was known previously in the state only from the summit of Mt. Baldy, 3476 m, also in the White Mountains, ca. 4.5 km SE of the Mt. Ord station (Tryon, Ann. Missouri Bot. Gard. 42:1–99, 1955). Tryon (op. cit.) cited material typical of this variety and also intermediates between vars. *scopulorum* and *densa* from the Mt. Baldy station.

Selaginella watsonii Underw. Coconino Co., Grand Canyon National Park, North Rim, Robbers Roost, 2530 m, 7 July 1951, *Merkle 254,* GCNP; Kanabonits Canyon, 2438 m, 9 Sep 1945, *Collom 1581,* ARIZ; Kanabownits Valley, 7 Sep 1949, *Collom s.n.,* GCNP; Kaibab Basin, 2499 m 5 Sep 1945, *Collom 1580,* ARIZ; Kaibab Basin, 2499 m, 31 Jul 1951, *Merkle 372,* GCNP. Mohave Co., Grand Canyon National Monument (now part of Grand Canyon National Park), head of Hack Canyon, tributary of Kanab Creek, 6 Jun 1968, *Gilbertson, Hevly and Mason M2790,* ARIZ, ASC, ASU. First state records. Previously known from SW Montana to NE Oregon, south to the southern border of Utah and southern California (Tryon, op. cit.).

I thank Dr. R. M. Tryon, Jr., for examining the cited specimens of *Selaginella.* The curators of the Arizona herbaria listed above have been most generous in permitting my use of their facilities and in loaning specimens.—Timothy Reeves, Department of Botany and Microbiology, Arizona State University, Tempe 85281.

NEBRASKA FLORA: NEW RECORDS.—As a result of field and herbarium studies, new records of plants found in western Nebraska are reported. All specimens cited, unless indicated otherwise, are at CSCN; all localities are in Nebraska.

Poa bulbosa L. Sioux Co., Sowbelly Canyon, Sowbelly Creek NE of Harrison, in *Fraxinus* and *Acer negundo* woodland near creek, sandy soil, abundant, 27 May 1974, *Spires 1024*. First record for Nebraska.

Ranunculus glaberrimus Hook. Dawes Co., ca 1 mi W of Chadron State Park on dirt road, Ponderosa pine forest, arroyo, in moist duff over dark clay loam soil with scattered limestone outcrops, small colony, 12 may 1974, *Spires and Morgan 942*; 13 Jun 1975, *Weedon and Morgan 7173* (NEB, KANU). These appear to be the first collections of this species for Nebraska. These collections represent an extension of the range of this buttercup 150 km southward from the Black Hills of western South Dakota and eastern Wyoming into the Pine Ridge of northwestern Nebraska.

Lithophragma parviflora (Hook.) Nutt. Dawes Co., 8 mi SE of Chadron on Hwy 20, then ca 0.5 mi E, *Ulmus* and *Fraxinus* floodplain woodland, sandy loam soil, scattered in shaded areas, 21 May 1973, *Spires 274*; 5 May 1974, *Spires 932*. Sioux Co., Sowbelly Canyon NE of Harrison, near Sowbelly Creek on floodplain under *Fraxinus* and *Acer negundo,* sandy soil, 27 May 1974, *Spires 1026*. These collections represent an extension of the range of this species 130 km southward into Nebraska from the Black Hills.

Ribes hirtellum Michx. Dawes Co., 8.0 mi SE of Chadron on Hwy 20, then ca 0.5 mi E on county road, elm-ash-boxelder-hackberry riparian forest, floodplain of Little Bordeaux Creek, sandy loam soil, rare, 24 May 1974, *Morgan 85;* 26 May 1975, *Morgan 228*. These collections represent an extension of the range of this gooseberry 130 km southward from the Black Hills into Nebraska.

Mentha spicata L. Box Butte Co., just E of Alliance, in a muddy slough, locally abundant, 25 Jun 1974, *Oduye 208*. First record for Nebraska.

Hyoscyamus niger L. Dawes Co., King's Canyon, S of Chadron, prairie habitat, 20 Jun 1971, *Urbatsch 466*; 3.7 mi E of Chadron on Hwy 20, then ca 8 mi S on dirt road, King's Canyon, Big Bordeaux Creek floodplain, elm and ash trees, sandy loam soil, scattered in roadside ditch, 8 Jun 1973, *Spires and Mason 381*; 19 Jun 1973, *Mason 245*. New for Nebraska.

Linaria dalmatica (L.) Mill. Dawes Co., Chadron, Catholic Cemetery, roadside ditch and cemetery lots, sandy loam soil, 6 Jun 1973, *Spires and Mason 350*; 15 mi S of Chadron on Hwy 385, 5 mi W on Table Road, then 3.0 mi N on Dead Horse Road, on roadside, steep slope, clay and sand, 28 Jun 1975, *Mazurka 78*. These collections represent an extension of the range of Dalmatian toadflax 160 km southward into Nebraska from the Black Hills.

This research was sponsored by grants from the Chadron State College Research Institute, David E. Spires and Ronald R. Weedon, investigators. We thank Steve Stephens of the State Biological Survey of Kansas for assistance in confirming the identification of specimens of *Ribes hirtellum*.—DAVID E. SPIRES, Department of Biology, University of Nebraska at Omaha, Omaha 68101 and WILLIAM T. MORGAN, Department of Entomology, Purdue University, West Lafayette, Indiana 47907.

JAMES FRANCIS MACBRIDE, 1892–1976.—J. Francis Macbride died on 16 Jun 1976 in Riverside, California, after being in failing health for two years. He was born on 19 May 1892 in Rock Valley, Iowa. He received an A.B. degree in 1914 from the University of Wyoming. For a while he was an assistant in the Gray Herbarium at Harvard. Later he was associated with the Field Museum in Chicago and is perhaps best known for his *Flora of Peru*. During the 1940's he moved to California and used the facilities of the University of California and Stanford University to continue his work on the *Flora of Peru*. Due to his efforts in photographing type specimens in Europe, all the information relative to types at Berlin-Dahlem was not lost.

GLINUS RADIATUS (AIZOACEAE), CHROMOSOME COUNT AND RANGE EXTENSION TO ARIZONA.—*Glinus radiatus* (Ruiz & Pav.) Rohrb. is a low, spreading, stellate-tomentulose, annual herb that occurs on banks of intermittent pools in desert habitats in Mexico, West Indies, Central America, South America, and Texas (Correll and Correll, *Aquatic and wetland plants of southwestern United States,* 1972). A collection from Baja California (*Brandegee*, no station cited) is mentioned by Wilson (N. Amer. Fl. 21:271. 1932) and Shreve and Wiggins (*Vegetation and flora of the Sonoran Desert,* 1964). This genus is not included in *Arizona flora* (Kearney and Pebbles, 1960), nor are any previous Arizona collections of *Glinus* on deposit in major Arizona herbaria. A small population of *G. radiatus* was recently discovered in Arizona: Maricopa Co., SE corner of sec. 2, T. 3N, R. 6E, Fort McDowell Quadrangle (USGS 7.5 minute series), 465 m, 22 Jun 1975, *Lane L1576* and *L1578,* ASU. The plants grew on slightly alkaline, gravelly, clay and loam soil on banks of an abandoned stock tank.

In October, 1975, an additional collection was made from the same population (*Keil and Lane L1785,* ASU), and buds were fixed in 4 chloroform: 3 ethanol: 1 glacial acetic acid (v:v), and stored in 70% ethanol. Anthers were stained in iron-acetocarmine and squashed in Hoyer's medium. The chromosome number was determined from meiotic microsporocytes to be $n = 9$. Mitra and Datta (Taxon 16:455. 1967) reported $n = 18$ for *G. lotoides* L. and *G. oppositifolia* (L.) DC.; Subramanyam and Kamble (Taxon 16:343. 1967) reported the same number for the latter species. This first count for *G. radiatus* indicates that the base number for the genus is $x = 9$.

We are grateful to Dr. D. J. Pinkava and Mrs. Elinor Lehto for their recognition of the original collection (*Lane L1576*) as a species not previously recorded for Arizona. MEREDITH A. LANE and DAVID J. KEIL, Department of Botany and Microbiology, Arizona State University, Tempe 85281.

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